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## THE MATURATION MITOSES IN CERTAIN PAEDOGENETIC PARASITES

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IN the course of reviewing the material for a general work on evolutionary processes in relation to cytology it has been necessary to consider the reduction or maturation division in a number of animal forms. This procedure was essential because of our lack of information in this important field, especially of a comparative nature. An important theme in this connection is the cytology of parthenogenesis. On the plant side the situation is clear and throughout, in cases of parthenogenesis, an extremely abnormal reduction division is found, presenting a detailed resemblance to the maturation mitoses of known hybrids. It has accordingly been very generally admitted in recent years on the botanical side, particularly for the higher plants, that parthenogenesis is intimately related to previous hybridization. In the case of animals the most important general situation is presented by those forms which are at once bisexual or hermaphrodite and at the same time parthenogenetic. Unfortunately, this group on the animal side is a very restricted one, since animals in general are unisexual. The forms most readily available in the present connection are the flat worms and such nematodes as are parthenogenetic. On account of lack of material the latter group has not been as yet investigated, but the present contribution will deal with the reduction division in tapeworms and flukes so far as it is illustrated in the

material already examined. It is important that these forms should be reinvestigated in the light of our greatly increased knowledge of the cytology of reproduction.

It will be convenient to begin with the common liver fluke, *Fasciola* (*Distomum*) *hepatica*. This is a form easily available on account of the fact that it is very commonly present in the liver of the domestic sheep. Various methods of preservation have been tried in this connection as the animal, as is common with parasites of this sort, is difficult to preserve adequately. Bouin and other formalin fluids have been used with indifferent results. The best preservation was obtained throughout with Carnoy's formula, 6 alcohol, 3 chloroform, and 1 glacial acetic acid. At first the worms were flattened before being treated with the reagent, but it was found that it was better to immerse them in the preservative and flatten out afterwards. After the material was washed in several changes of strong alcohol it was transferred to equal parts of alcohol and glycerine in which it was left for a few hours. Subsequently the animals were laid down on stiff pieces of cardboard and an abundance of 6 per cent. nitrocellulose was dropped over them. After the nitrocellulose had dried slightly, a piece of heavy paraffined paper of the same size as the cardboard was laid over the animal, then a glass slide on which were placed lead weights to flatten the creature. After the nitrocellulose had set, holding the object firmly to the card, the paraffined paper was wrapped around in two directions with fine white thread, number 50 or 60 gauge. The objects were then dropped into strong alcohol and afterwards pricked with a fine needle, No. 12, mounted in a cork. The pricking is for the purpose of allowing perfect penetration of the nitrocellulose and is essential for obtaining the very thin sections which are necessary. After the worms have been pricked they are put into absolute alcohol and carefully pumped with an efficient air-pump. The ordinary water-pump is not powerful enough for satisfactory results and an electric pump

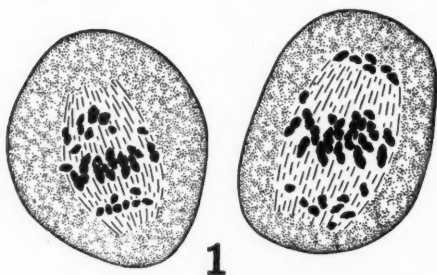
must be used for good results. The material is then run up on the cards in nitrocellulose and embedded after the manner described recently by the present author.<sup>1</sup> After embedding, the sections were made with a sliding microtome and these should be 5 micra or thinner. The most satisfactory stain was Heidenhain's iron haematoxylin. Counter-staining was not found advantageous, as it tends to obscure the details of mitosis. The figures are fairly large in this form and have already been the subject of investigation in recent years by Schellenberg.<sup>2</sup> Just as in the famous case of *Drosophila melanogaster*, however, his investigations lacked the background of recent developments in the general cytology of meiosis, particularly in plants. The tendency in the past has been to disregard abnormalities in the reduction division and to search for figures which were normal in character. This tendency was quite correct before the cytology of known hybrids and variable species had become as familiar as it is at the present time. It may be stated in a general way that there are many abnormalities in the meiosis of *Fasciola hepatica*. There is also a great deal of sterility, many of the clusters of mother cells breaking down in the course of development. Both the irregularities and the sterility found here are of the type characteristic of known hybrids.

Fig. 1 shows two typical primary spermatocytes of the species under discussion in the metaphase. It can readily be seen that, in the two cells figured, a number of bivalent chromosomes are clustered more or less regularly at the equator of the spindle, whilst towards the poles lie a considerable number of univalents. This mode of division is extremely abnormal and exactly duplicates that found in known hybrids.

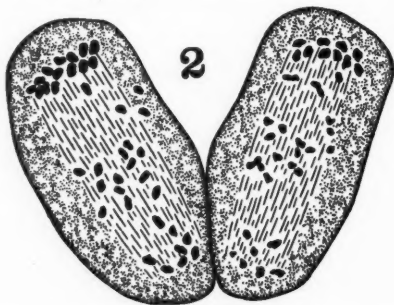
Fig. 2 shows the anaphase in two elongated cells which converge. The plane of section has removed some of the

<sup>1</sup> "Technical Contributions," *Botanical Gazette*, lxxxvi, 4, December, 1928.

<sup>2</sup> *Arch. f. Zellf.* 6: 443-484, pls. 24-36.

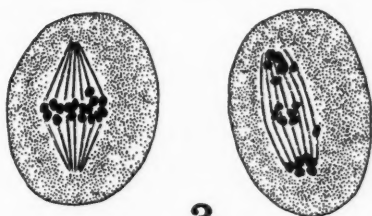


chromosomes at the lower ends of the two spindles. In the upper region numerous univalent chromosomes are present. Additional univalents are scattered on the spindle in the region between the poles. Here again we have the type of anaphase which is characteristic of hybrids and variable species.



The division of the secondary spermatocytes is much more regular and in the metaphase it is very often difficult to catch any lagging chromosomes. These are more commonly seen in the anaphase, as is shown in Fig. 3.

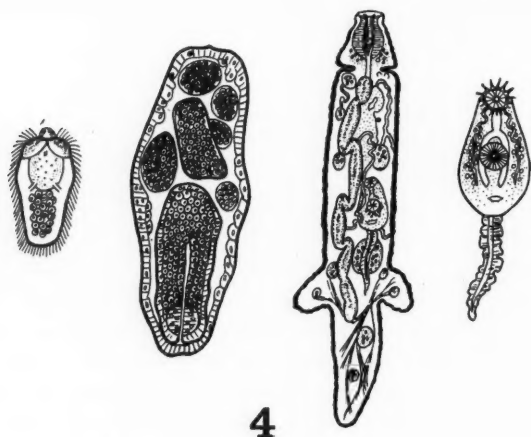
It will be seen from the above that in many cases the reduction division in the common liver fluke is extremely abnormal and presents those features which are characteristic of hybrids. It has been objected that occasional abnormalities are of slight importance. To this it can be replied that in known hybrids there is a considerable variety of variability in the meiotic mitoses. Some of these are quite normal, whilst others present varying de-



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gresses of abnormality. Often in hybrids it becomes necessary to search for the abnormal meiotic features which may be present in such forms. The present writer has pointed out that, however irregular the meiotic divisions may be, in hybrid forms the somatic mitoses are in general extremely regular. This general situation is of course important in connection with the known greater stability of forms of somatic origin.

It will be well at this stage to refer in some detail to the life history of the common liver fluke, *Fasciola hepatica*. The eggs, on reaching water, develop into a ciliated embryo (Fig. 4, first from left) which contains a rudimentary ovary internally. These ciliated forms swim about in water or make their way over the surface of vegetation bordering water, whence they penetrate into the bodies of snails. They are, for example, common in our larger Limnaeas. Here the ciliated form develops into a so-called sporocyst (Fig. 4, second from left). From its rudimentary ovary develop embryos parthenogenetically. Since the mother is immature the parthenogenesis in this case comes under the heading of paedogenesis or infantile reproduction. The embryos formed inside the sporocysts escape and in general give rise to a somewhat higher type known as redia (Fig. 4, third from left) which possesses, contrary to the sporocyst, a sucker and a rudimentary intestine. Inside the redias are produced tailed forms with hooks and suckers known as Cercaria (Fig. 4, fourth from left). These, in contrast to the preceding phases, are quite active and escape from the snail, becoming encysted on grasses, etc.



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Sheep eating these grasses absorb the encysted Cercariae, which develop into the completely sexual stage known as the liver fluke, *Fasciola hepatica*. This condition of heterogenesis is extremely common in parthenogenetic animals, being exemplified by many species of insects, such as Aphids, Hymenoptera, etc. The cytology of these forms is being reinvestigated in the light of more recent developments, and an account of it will be published in a subsequent article. It may be stated preliminarily that the results obtained entirely correspond with those found in parthenogenetic plants.

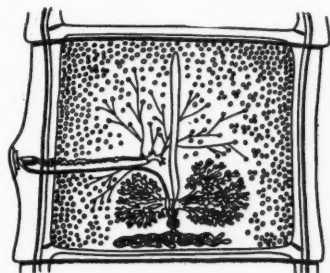


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Fig. 5 shows the mature animal of the common liver fluke, *Fasciola hepatica*. The only details of structure which need be emphasized in the present connection are the organs of reproduction. In the upper part of the figure is shown the much convoluted ovarian system containing the young and developing eggs. Mainly in the lower part of the figure and in the

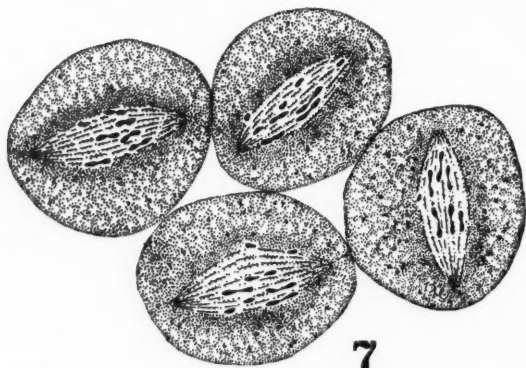
center of the body are found the much branched testicular organs. It is these which show most conveniently the maturation divisions in material fixed in the appropriate stages.

We may now turn our attention to the situation in tapeworms. Fig. 6 shows the general organization of



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one of the segments in a tapeworm. Obviously, as in the fluke, the two kinds of reproductive organs are present in the same animal. Commonly the sperms develop more rapidly than the eggs, and in a fully matured segment of a tapeworm the spermaries are no longer present, the body being occupied mainly by developing eggs. Fig. 7 shows the meiotic conditions as illustrated by primary spermatocytes of *Moniezia expansa*, the common sheep tapeworm. The sperm mother cells in tapeworms, so far as they have been observed by the present writer, are extremely small and the reduction division is correspondingly difficult to discern. By using very thin sections, extremely brilliantly stained, it has been possible, however, to make out the essential features in the first division of the spermatocytes. Fig. 7 shows such a division extremely highly magnified by the use of a millimeter and a half Zeiss oil immersion, a reasonably powerful ocular, and a powerful ribbon filament light. It is clear that in all the four cells depicted in the drawing there is striking irregularity present. The chromosomes are in general bivalents, although some univalents seem



to be present. Instead of being gathered in the equator of the cell as is the normal situation for bivalents, and thus constituting the normal metaphase, they lie in various positions on the spindle and present in fact the atypical reduction division which is characteristic of many known hybrid plants. A similar condition has been described by the present author in the case of *Drosophila melanogaster*.<sup>3</sup> The results in this case at first were strongly questioned by other observers, but now there is general agreement that the present author's results are correct, although there is still difference of opinion as to the conclusions which should be drawn from the extremely abnormal mitoses of this much investigated species.

The anaphase in the case of *Moniezia* is difficult to catch, but the same disorderly arrangement of chromosomes, which are now for the most part univalent, is present also in this stage. The secondary spermatocytes are so minute that it is extremely difficult even with the highest power to make out clearly the details of mitosis. It has not been thought necessary to figure them in the present connection, especially as the divisions of the secondary spermatocytes are in general much more regular than those of the primary ones.

<sup>3</sup> "Evidence as to the Cause of So-called Mutations in *Drosophila*," *Genetica*, vii: 273-286.

It will be clear, if the above descriptions are correct, that in *Moniezia* extreme irregularities are present in the reduction division. An ever wider range of accumulated facts makes it more and more obvious that abnormalities in the reduction or meiotic or maturation divisions in plants and animals are of the greatest theoretical importance from the standpoint of the doctrine of descent. It is of interest to note in the case of the tapeworm under discussion that the reduction divisions present a close parallel to the reduction divisions in parthenogenetic flowering plants such as the dandelion, the hawkweed, the fleabane, the broomrape, etc., etc. It is practically universally conceded that the abnormalities in meiosis in hybrid flowering plants indicate hybrid origin for such forms. There can be little doubt that a similar conclusion should be drawn in the case of the paedogenetic parasites under discussion at the present time.

It will be of interest in the present connection to discuss the general relations of so-called diplogenesis. This phenomenon is presented by aphids, bees, wasps, flukes, tapeworms, etc., etc. It is sometimes not very aptly designated an alternation of generations. That term is best restricted to the conditions found in plants where there is a distinct alternation of generations, the two being, in general, cytologically distinct from one another. In the case of diplogenesis, however, although the method of reproduction varies from parthenogenetic to sexual between the phases, the cytological constitution in both types is the same. The diplogenesis of the Hymenoptera, aphids, etc., differs from that in the forms under discussion in the present article in one very important respect. The first-named forms are unisexual, whilst the parthenogenetic types under discussion in the present article are hermaphrodite. That constitutes an important difference and its theoretical significance has been recently pointed out by Wilson:

*"Special Peculiarities of the X-chromosome:* In the earlier stages of development, and in the division of the

somatic cells generally, the X-chromosome does not, so far as known, differ in behavior from the others, nor do the two sexes differ in this respect. In later stages, on the other hand, the X-chromosome in the male germ-line shows certain special peculiarities of behavior which sometimes appear in the spermatogonia and are almost always present in the spermatocytes. In the female line these differences do not exist, or are much less marked."<sup>4</sup>

It is to be emphasized that Wilson has noted the distinction between the conduct of the chromosomes in the meiotic mitoses of parthenogenetic forms and the somatic mitoses. As far as the writer is aware he is the only zoologist who has clearly emphasized this important difference. The present writer on several occasions has pointed out that in known hybrids, however irregular the meiotic mitoses may be, the somatic divisions are in general quite normal. This parallelism suggests a fruitful comparison. It is very generally held on the plant side that parthenogenesis and indeed also apogamy are a sequel of hybridization. It would be strange if a different situation were presented by animals, especially as there is an enormous amount of supporting evidence for the hybrid hypothesis on the plant side. Wilson remarks, as indicated above, that the test of the sex chromosome theory of parthenogenesis, as held generally by zoologists, is presented by the meiotic mitoses in hermaphrodite animals. It will probably be clear to the reader who has perused the foregoing paragraphs that in the outstanding hermaphrodite types illustrated by the flukes and tapeworms the same lagging chromosomes are present as in unisexual forms. It clearly follows that such lagging chromosomes can not be properly regarded as sex chromosomes but that the most reasonable interpretation of them is that they constitute an abnormality following previous hybridization. This general statement seems to cover, however, only sex chromosomes of the

<sup>4</sup> "The Cell in Development and Heredity." The Macmillan Company, New York. Third edition, with corrections. 1928.

univalent type. In those sex chromosomes which are represented by a diverse pair it is quite likely that there is some relation between the chromosomes and the function of sex. It will probably turn out to be true in the long run that all univalent sex chromosomes should not be designated as such, but should be considered as lag-gards indicating previous hybridization.

It would seem probable, then, that the cytological investigation of meiosis, in the two representative forms described in the present article, indicates that for animals as well as plants the explanation of parthenogenesis is previous hybridization. Although there may be a possible doubt in the case of unisexual animals, there can scarcely be any question where hermaphrodites such as *Fasciola* and *Moniezia* are concerned. When an extensive study of aphids has been completed it will be clear that current zoological hypothesis of parthenogenesis even in this group as dependent on sex chromosomes must be abandoned because of its unworkability.

The general investigation of meiosis in plants and animals seems to be destined to throw an extremely important light on the cause of evolutionary change. In the case of many animals and plants the maturation divisions are of what may be called a normal type, in which there are regular metaphases and anaphases. A marked departure from regularity is found in both hybrid and parthenogenetic types. It seems appropriate on the evidence here supplied to add to these diplogenetic and paedogenetic forms such as the tapeworms and flukes.

## CHICK MORTALITY AND SEX-RATIO IN THE DOMESTIC FOWL

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It is a well-known fact that in man during childhood male mortality is higher than female mortality. This greater male mortality is responsible for a gradual decline of the sex-ratio from birth to puberty.

It appears that no observations have been made as yet concerning the relation between postnatal mortality and sex-ratio in the domestic fowl. Since such information aside from its immediate interest may be of theoretical value for the explanation of selective mortality in general, we have undertaken to analyze the mortality records for the first two months after hatching of the chicks, which at this station were hatched for experimental purposes during the years 1922 to 1930. Approximately 19,100 chicks were hatched during this nine-year period. About 9,500 chicks out of this total belonged to a large number of crosses which were made for the genetic analysis of various morphological characters, while the remaining 9,600 chicks were Single Comb White Leghorns. The Leghorn chicks belonged to inbreeding experiments carried out by Dr. L. C. Dunn and were partly derived from brother by sister or half-brother by sister matings and partly from crosses between unrelated individuals.

In tabulating the death records all cases of accidental death (due to crowding, predatory enemies, drowning, and so on) were omitted; these amounted to approximately 5 per cent. of the total mortality. There was also a small number of chicks which could not be sexed because they had lost their identification bands or were decomposed before they were found. Most of the chicks were hatched during March, April and May. There were some small hatches, however, which came off in January

TABLE I  
MORTALITY RECORDS OF CROSS-BRED CHICKS 1922-1930  
SEX-RATIO (PER CENT. OF MALES) AMONG CHICKS WHICH DIED DURING THE FIRST TWO MONTHS OF LIFE  
9,500 chicks were hatched and the sex was recorded of 2,329 chicks dying from natural causes during the first two months of life

Year	First week			Second to fourth week			Fifth week to end of second month		
	Males	Females	Percentage males	Males	Females	Percentage males	Males	Females	Percentage males
1922 .....	19	14	58	91	61	60	27	31	47
1923 .....	46	36	56	212	198	52	40	31	56
1924 .....	14	9	61	83	58	59	40	46	47
1925 .....	12	4	75	40	46	47	35	30	54
1926 .....	9	8	53	26	32	45	37	23	62
1927 .....	28	20	58	51	39	57	51	40	56
1928 .....	23	19	55	45	55	45	40	39	51
1929 .....	29	36	45	72	57	56	28	28	50
1930 .....	66	65	50	53	54	50	16	17	49
Totals .....	246	211	53.8	673	600	52.9	314	285	52.4

and February and in June and July. These were included, since several authors have shown that there is no significant seasonal variation in the sex-ratio of hatching chicks (Lambert and Knox, Horn, Lambert and Curtis). The mortality was tabulated separately for the first week after hatching, the second to fourth week, and from the beginning of the fifth week to the end of the second month of postnatal life. After the second month chick mortality usually was low and it was not expected that sufficient numbers could be accumulated from our records to detect significant differences between male and female mortality.

Tables I and II give the actual figures of males and females and the percentages of males which died in each year among the cross-bred and the White Leghorn chicks. The cross-breds with a total mortality of 2,329 chicks had a sex-ratio of dead chicks of 53.8, 52.9 and 52.4 per cent., respectively, during the first week, the second to fourth week, and the fifth week to the end of the second month intervals. The corresponding figures for the sex-ratio of dead chicks among 3,354 Leghorn chicks are 52.8, 51.6 and 54.6 per cent., respectively. For the combined material we have records of 5,683 dead chicks (from a total of 19,100 chicks hatched) with the following distribution:

	Males	Females	Percentage males	Difference from 50% P. E. of diff.
First week .....	539	473	$53.3 \pm 1.06$	3.1
Second to fourth week .....	1676	1541	$52.1 \pm 0.59$	3.7
Fifth week to end of second month .....	781	673	$53.7 \pm 0.88$	4.2

The departures of these sex-ratios from equality exceed at least slightly three times their probable error. During the entire period of the first two months of life the male mortality amounted to  $52.7 \pm 0.45$  per cent. This devia-

TABLE II  
MORTALITY RECORDS OF LEGHORN CHICKS 1922-1929  
SEX-RATIO (PER CENT. OF MALES) AMONG CHICKS WHICH DIED DURING THE FIRST TWO MONTHS OF LIFE  
9,600 chicks were hatched and the sex was recorded of 3,354 chicks dying from natural causes during the first two months of life

Year	First week			Second to fourth week			Fifth week to end of second month		
	Males	Females	Percentage males	Males	Females	Percentage males	Males	Females	Percentage males
1922 .....	14	6	70	45	32	58	54	34	61
1923 .....	37	29	56	85	87	49	30	30	50
1924 .....	65	43	60	453	396	53	134	110	55
1925 .....	42	40	51	141	148	49	138	129	52
1926 .....	16	18	47	43	51	46	29	11	73
1927 .....	32	36	47	66	64	51	28	25	53
1928 .....	11	14	44	87	76	53	39	33	54
1929 .....	76	76	50	83	87	49	15	16	48
Totals .....	293	262	52.8	1003	941	51.6	467	388	54.6

tion from equality amounts to six times its probable error.

The significance of these deviations from chance mortality is considerably strengthened by the fact that there was a slight deficiency of male chicks already at hatching time. Dr. L. C. Dunn in an (unpublished) analysis of a part of the data used in this report found among a total of 5,421 Leghorn chicks 2,633 males and 2,788 females, corresponding to a sex-ratio of  $48.57 \pm 0.46$  per cent. males. Among 2,638 cross-bred chicks he found 48.59 per cent. males. These figures are in close agreement with those reported by other investigators.<sup>1</sup>

The sex records for the mortality of chicken embryos are conflicting. Some authors (Lambert and Knox, Horn) found a higher mortality of males, while others (Jull, Lambert and Curtis) observed a greater female mortality. Probably in no case a sufficient number of embryos has been observed to detect significant deviations from an equal mortality of the two sexes. If in the fowl there is equality of the sexes at fertilization (primary sex-ratio), as all authors seem to assume, then the significant deficiency of males among almost 68,000 chicks observed at hatching time would suggest that there is a slight majority of males among the embryos which die. At any rate, it seems safe to say that if any differential mortality occurs during embryonic development of chickens, it is the male sex which suffers more; if this is so, the same conditions which from our records appear to prevail in postnatal life, would already exist before hatching.

<sup>1</sup> The combined figures of all available observations (Darwin, Field, Pearl, Crew and Huxley, Jull, Mussehl, Lambert and Knox, Horn, Lambert and Curtis, Dunn, Callenbach, Christie and Wriedt, and Jull) of the sex of chicks at hatching amount to 67,993 chicks with 33,162 males, corresponding to  $48.77 \pm 0.13$  per cent. males. This deficiency of males exceeds nine times its probable error, and it can not be doubted, therefore, that in general there is already a deficiency of male chicks at hatching time.

It appears that no evidence is available at present which can be used for the explanation of the greater male mortality among human infants. Lenz, Huxley and Schirmer have put forward the hypothesis that recessive sex-linked factors with a slightly deleterious effect upon the viability account for the greater male mortality. Huxley says: "Since the male mammal is heterogametic, any recessive factor borne in the X-chromosome will take effect in all males carrying them, whereas in females both sex-chromosomes must carry the factor before the corresponding characters appear." Huxley believes that circumstantial evidence for the correctness of his explanation is to be found in the fact that adverse conditions seem to intensify, favorable ones to neutralize the differential male mortality during pregnancy (Parkes, Punnett). Furthermore, he thinks that this explanation "also provides a basis for the fact that male secondary sex-ratio is higher in the offspring of young than of old mothers and higher in first births, decreasing at each subsequent pregnancy." The lower male secondary sex-ratio of illegitimate children and the higher one of the Jewish population, Huxley likewise explains with this hypothesis, assuming that differences in prenatal care will aggravate or counteract to a certain extent the harmful effects of recessive sex-linked factors. The higher percentage of males found by Little (and before him by Pearl and Pearl) among children of wide racial crosses as compared with the sex-ratio of relatively pure stock is explained by Huxley as being due to heterosis, "enabling the males to resist the deleterious effect of harmful sex-limited factors."

If harmful sex-linked factors are assumed to be the cause of higher male mortality in human infants (and embryos), then we should expect to find the reverse situation, higher female mortality, in animals like chickens in which the females are the heterogametic sex. Actually, however, we saw that in chickens as in man the post-

natal mortality is higher in males than in females. If there is in chickens any differential mortality during embryonic development, as is suggested by the significant deficiency of males at hatching, then again it appears that the situation is the same as in man. In view of our evidence from chickens the general explanatory value of the hypothesis of Lenz, Huxley and Schirmer becomes rather doubtful, although it is quite possible that sex-linked factors play a minor rôle as a cause of differential mortality. We must look for an explanation which can be applied equally well to man and fowls.

For most, if not all, classes of higher animals it appears to be characteristic that the males have a higher basal metabolism than the females. The work of Riddle and others makes it probable that this metabolic difference in one way or another already begins during embryonic development. The life span of any mechanical engine under otherwise constant conditions depends upon the speed at which it is run. Speed that falls above or below the optimum means greater wear.<sup>2</sup> The assumption that generally the basal metabolism of the female sex approaches optimal conditions more closely than that of the male would furnish an explanation for the greater infant mortality of organisms as far apart as man and domestic fowls. In a physico-chemical system the life span of a mechanism under otherwise constant conditions varies with the rate at which reactions take place. Seen from this view-point, the male again would be at a disadvantage. The acceleration of chemical reactions corresponding to the higher metabolic rate must mean greater wear on the physical parts of the organic machine. It appears also from recent work with pigeons (Riddle, Christman and Benedict) that the basal metabolism of males is more easily and to a greater extent upset by unfavorable conditions than is that of

<sup>2</sup> There are probably engines in which the optimum is at or near the minimum speed. This, however, is taken as a special case of the general rule.

females. This finding points to the conclusion that in the male organism processes take place with a lesser degree of stability which again would involve a greater amount of wear through necessary readjustments. There is considerable evidence in favor of such an explanation of the differential mortality of males and females, most of which may be found in Joyet-Lavergne's recent book. Working with *Daphnia magna* MacArthur and Baillie found that the males have a higher metabolic rate than the females. They found, furthermore, that the males of this species have a more rapid heart beat than the females. On the basis of this and other evidence MacArthur and Baillie suggest that the shorter life span of the males of *Daphnia magna* is to be explained as a consequence of the existing metabolic differences.

In addition to this instance in which a direct association could be demonstrated to exist between the metabolic rate and the speed of functioning of an organ there is ample evidence for the conclusion that the higher metabolic rate of males is not compensated by a different organization of the organism, but is actually brought about by a more rapid or more continuous functioning of the organs and cells of the male body. Most of the work, for instance, that has been done in connection with Manoi-loff's reaction points to this conclusion.

It appears that there are no observations on record which are inconsistent with the assumption that the higher metabolic rate of males is produced by a more rapid or more continuous performance of organs and cells of the male organism, and if the latter conclusion is valid, our comparison between the life span of organisms and of mechanical engines appears reasonable.

The observations which Lenz, Huxley and Schirmer adduce to strengthen their hypothesis would fit equally well into an explanation on the basis of differences in metabolism—as, in fact, they would fit into almost any other physiological explanation. Until new evidence is

forthcoming, these sexual differences in the rate and stability of metabolism are offered as a working hypothesis for the understanding of differential mortality in the two sexes.

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## LINKAGE IN SIZE INHERITANCE

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IN reports of a previous investigation on size inheritance and growth in a mouse species cross, the author (1930, 1931) noted indications of linkage between general size and color characters. Since such linkage had never been demonstrated in mammals it was considered advisable to continue work along this line in an effort either to confirm or to disprove its presence.

The animals used in the present investigation were of the same stocks as those previously employed: a small Chinese species, *Mus bactrianus*, and a large inbred race of *Mus musculus*. The former when adult weigh but little more than half as much as the latter, while all other quantitative characters studied likewise have lower values. Tables showing mean values for quantitative indices of the two species were given in one of the papers cited (1931). The two forms still retain the same relationships, although for some reason not clearly understood the absolute values of both are now lower.

In addition to size differences the smaller species possesses the dominant color genes for white bellied agouti ( $A^w$ ), black (B) and intensity (D); while the larger has the recessive allelomorphs, non-agouti (a), brown (b) and dilution (d). Herein lies an especial advantage for the detection of linkage. Since recessive genes are generally more deleterious than dominant, any tendency of our back-cross mice to vary in the direction of their respective parental types can not be attributed to the beneficial effects of dominant genes.

Since the purpose of the renewed investigation was the demonstration of linkage—if such existed—between quantitative and qualitative characters, the back-cross generation was used almost exclusively, with in addi-

tion, however, a small  $F_2$  generation. The back-cross was made in only one way. *Musculus* females were mated to  $F_1$  males, all of which in turn were the product of *musculus* mothers and *bactrianus* fathers. All back-cross and  $F_2$  animals were born between July 10 and December 29, 1930. Diet and care were kept uniform throughout the experiment. The mice were killed between the 181st and the 184th day and the external measurements taken immediately after death. The leg bones and the skulls were cleaned of flesh by boiling in a solution of ammonium, phenol and water. After the cleaned bones had dried at least two days in the open air the skeletal measurements with the exception of skull width (interorbital width) were taken with a Starrett bench micrometer to the nearest .01 mm. For skull width vernier calipers were used, the value being recorded to the nearest .1 mm. The author personally prepared all the bones and made all the measurements, thus reducing the personal error incident to more than one observer and recorder.

The quantitative characters reported on in this paper comprise the following: weight on the first, eleventh, thirty-first, sixty-first, ninety-first, one hundred twenty-first, one hundred fifty-first and one hundred eighty-first day; body length, tail length, skull length, skull width, humerus length, femur length, tibia length and cranial capacity. These measurements are described in an earlier paper by the author (1931a), so detailed descriptions are unnecessary here.

As before mentioned, the existence of linkage of size—relating to the organism as a whole and not to a particular part—with color characters has never been conclusively proved in mammals. Castle (1929) could find no evidence for it in rabbits, nor could Livesay (1930) in rats. Among plants, Lindstrom (1926), for example, found fruit color linked with fruit size in tomatoes. The same author (1929) showed that the number of rows in the maize ear was associated in inheritance with several

simple mendelizing characters such as cob-color and endosperm color. These examples, however, are perhaps scarcely comparable with the usual situation in mammals, since they refer to a particular part of the organism rather than to the general size, of which weight, body length and bone lengths are more or less satisfactory manifestations.

If, in our investigation, the "tagged" *musculus* chromosomes carrying the recessive genes for color also possess genes influencing size then the back-cross mice with the recessive factors will tend to be larger than those with the dominant allelomorphs. If quantitative characters are not inherited through chromosomal genes or if no such genes are present on the three chromosomes investigated the recessive members of the factor pairs will exhibit no tendency to exceed the dominant. Thus in determining the presence or absence of linkage, all agouti back-cross mice were compared with all non-agouti, in regard to each of the quantitative characters. Similarly, blacks were compared with browns and intense animals with dilute. The sexes, of course, were considered separately.

Tables I and II present these mean values as well as the means for the total population of that generation. None of the mice were used for breeding, so all females included were virgins.

Table III presents a summary of the significant differences in adult quantitative characters between the recessive and dominant members of the factor pairs. A difference as great as or greater than four times its probable error is considered significant.

In the matter of weight, brown mice of both sexes are significantly heavier than blacks at the age of 181 days. A perusal of Table I, however, shows that this condition does not prevail at all ages, since in early life the situation is reversed, perhaps because of the initial effects of the dominant gene. In neither of the other factor pairs is there a significant difference in adult weight.

TABLE I  
COMPARATIVE WEIGHTS OF DIFFERENT CLASSES OF BACK-CROSS MICE

Class	1st day			Weight (gms)			11th day			Weight (gms)			31st day			Weight (gms)			61st day			Weight (gms)		
	No.	Mean	δ	No.	Mean	♀	No.	Mean	δ	No.	Mean	♀	No.	Mean	δ	No.	Mean	♀	No.	Mean	δ	No.	Mean	♀
Agouti	85	1.36 ± .014		70	1.29 ± .015		85	5.12 ± .071		70	4.89 ± .075		85	9.19 ± .150		70	8.44 ± .150		85	15.2 ± .16		70	13.3 ± .15	
Non-agouti	67	1.30 ± .014		70	1.23 ± .015		68	4.96 ± .056		70	4.76 ± .059		68	8.57 ± .148		70	8.26 ± .129		68	14.9 ± .18		70	13.3 ± .14	
Black	81	1.37 ± .014		62	1.28 ± .016		81	5.24 ± .070		62	4.90 ± .073		81	8.93 ± .159		62	8.16 ± .144		81	14.8 ± .17		62	13.1 ± .15	
Brown	71	1.30 ± .014		78	1.24 ± .015		72	4.84 ± .057		78	4.76 ± .064		72	8.81 ± .134		78	8.49 ± .135		72	15.4 ± .16		78	13.5 ± .13	
Intense	81	1.35 ± .014		67	1.27 ± .015		82	5.08 ± .059		67	4.82 ± .067		82	9.05 ± .147		67	8.15 ± .143		82	15.1 ± .16		67	13.0 ± .14	
Dilute	71	1.31 ± .014		73	1.25 ± .016		71	5.02 ± .075		73	4.83 ± .069		71	8.76 ± .154		73	8.52 ± .136		71	15.0 ± .18		73	13.6 ± .15	
Total	152	1.33 ± .009		140	1.26 ± .011		153	5.05 ± .047		140	4.82 ± .048		153	8.91 ± .113		140	8.34 ± .099		153	15.1 ± .12		140	13.3 ± .10	

Class	91st day			Weight (gms)			121st day			Weight (gms)			151st day			Weight (gms)			181st day			Weight (gms)		
	No.	Mean	δ	No.	Mean	♀	No.	Mean	δ	No.	Mean	♀	No.	Mean	δ	No.	Mean	♀	No.	Mean	δ	No.	Mean	♀
Agouti	85	16.8 ± .16		70	15.0 ± .17		85	18.6 ± .17		70	16.8 ± .18		85	20.1 ± .16		70	18.1 ± .24		85	21.4 ± .20		70	19.2 ± .27	
Non-agouti	68	17.2 ± .21		70	15.0 ± .15		68	18.9 ± .25		70	16.9 ± .17		68	20.6 ± .28		70	18.5 ± .22		68	23.0 ± .30		70	19.7 ± .26	
Black	81	16.4 ± .17		62	14.4 ± .18		81	18.2 ± .18		62	16.0 ± .17		81	19.6 ± .20		62	17.3 ± .19		81	21.0 ± .22		62	18.3 ± .24	
Brown	72	17.6 ± .18		78	15.6 ± .14		72	19.4 ± .23		78	17.5 ± .16		72	21.0 ± .22		78	19.1 ± .24		72	22.8 ± .26		78	20.4 ± .25	
Intense	82	17.1 ± .17		67	14.7 ± .16		82	18.9 ± .22		67	16.6 ± .17		82	20.4 ± .21		67	18.0 ± .25		82	21.9 ± .26		67	19.3 ± .27	
Dilute	71	17.0 ± .18		73	15.4 ± .16		71	18.6 ± .19		73	17.0 ± .18		71	20.2 ± .22		73	18.6 ± .22		71	21.5 ± .23		73	19.6 ± .26	
Total	153	17.0 ± .13		140	15.1 ± .12		153	18.8 ± .15		140	16.8 ± .12		153	20.3 ± .15		140	18.3 ± .16		153	21.7 ± .17		140	19.5 ± .19	

TABLE II  
COMPARATIVE MEASUREMENTS OF DIFFERENT CLASSES OF BACK-CROSS MICE

Class	Skull length (mm)			Skull width (mm)			Humerus length (mm)			Femur length (mm)						
	No.	♂ Mean	♀ Mean	No.	♂ Mean	♀ Mean	No.	♂ Mean	♀ Mean	No.	♂ Mean	♀ Mean				
Agouti .....	85	21.06 ± .036	69	20.93 ± .040	85	3.80 ± .008	70	3.81 ± .009	85	11.02 ± .028	69	10.71 ± .027	85	14.28 ± .042	69	14.15 ± .038
Non-agouti .....	68	20.95 ± .032	70	20.86 ± .043	68	3.77 ± .010	70	3.79 ± .010	67	10.88 ± .028	70	10.57 ± .030	66	14.16 ± .035	69	14.06 ± .041
Black .....	81	20.98 ± .037	62	20.85 ± .045	81	3.78 ± .008	62	3.80 ± .010	80	10.83 ± .028	62	10.52 ± .029	80	14.08 ± .038	62	13.95 ± .031
Brown .....	72	21.05 ± .033	77	20.93 ± .037	72	3.80 ± .010	78	3.80 ± .009	72	11.10 ± .026	77	10.74 ± .027	71	14.39 ± .037	76	14.24 ± .037
Intense .....	82	20.96 ± .036	66	20.80 ± .033	82	3.78 ± .008	67	3.78 ± .010	81	10.91 ± .030	66	10.61 ± .027	82	14.16 ± .038	66	14.05 ± .038
Dilute .....	71	21.07 ± .034	73	20.98 ± .043	71	3.79 ± .010	73	3.82 ± .009	71	11.02 ± .028	73	10.67 ± .031	69	14.30 ± .040	72	14.16 ± .041
Total .....	153	21.01 ± .025	139	20.90 ± .029	153	3.79 ± .007	140	3.80 ± .007	152	10.96 ± .021	139	10.64 ± .021	151	14.22 ± .028	138	14.11 ± .028
<hr/>																
	Tibia length (mm)			Body length (mm)			Tail length (mm)			Cranial capacity (gms of Hg.)						
	No.	♂ Mean	♀ Mean	No.	♂ Mean	♀ Mean	No.	♂ Mean	♀ Mean	No.	♂ Mean	♀ Mean	No.	♂ Mean	♀ Mean	
Agouti .....	85	16.27 ± .043	70	15.97 ± .037	85	89.2 ± .24	70	88.2 ± .23	83	86.3 ± .35	68	85.0 ± .42	85	5.15 ± .019	69	5.19 ± .024
Non-agouti .....	67	16.08 ± .034	69	15.83 ± .042	68	89.0 ± .25	70	88.4 ± .27	66	86.9 ± .42	67	85.3 ± .43	68	5.09 ± .021	70	5.10 ± .024
Black .....	80	16.08 ± .041	62	15.76 ± .042	81	88.4 ± .25	62	87.5 ± .27	80	86.8 ± .37	59	84.9 ± .46	81	5.15 ± .021	62	5.17 ± .026
Brown .....	72	16.30 ± .036	77	16.02 ± .036	72	89.9 ± .21	78	89.0 ± .23	63	86.3 ± .40	76	85.4 ± .39	77	5.09 ± .019	77	5.13 ± .023
Intense .....	81	16.09 ± .039	66	15.81 ± .038	82	88.5 ± .25	67	87.6 ± .23	78	85.0 ± .33	65	84.3 ± .37	82	5.11 ± .020	66	5.10 ± .021
Dilute .....	71	16.30 ± .038	73	15.98 ± .040	71	89.9 ± .22	73	89.0 ± .26	71	88.2 ± .40	70	86.0 ± .45	71	5.13 ± .020	73	5.18 ± .026
Total .....	152	16.18 ± .028	139	15.90 ± .028	153	89.1 ± .17	140	88.3 ± .18	149	86.6 ± .27	135	85.2 ± .30	153	5.12 ± .014	139	5.15 ± .017

TABLE III  
COMPARISON OF RECESSIVE AND DOMINANT MEMBERS OF FACTOR PAIRS. ADULT QUANTITATIVE CHARACTERS OF BACK-CROSS MICE

Character	Recessive	Mean	Dominant	Mean	Difference	Difference Probable error
Weight, 181st day	Brown ♂ ♂ Brown ♀ ♀	22.8 ± .26 gms 20.4 ± .25 gms	Black ♂ ♂ Black ♀ ♀	21.0 ± .22 gms 18.3 ± .24 gms	1.8 ± .34 gms 2.1 ± .35 gms	5.3 6.0
Skull length	No significant differences					
Skull width	No significant differences					
Humerus length	Brown ♂ ♂ Brown ♀ ♀	11.10 ± .026 mm 10.74 ± .027 mm	Black ♂ ♂ Black ♀ ♀	10.83 ± .028 mm 10.52 ± .029 mm	.27 ± .038 mm .22 ± .040 mm	7.1 5.5
Femur length	Brown ♂ ♂ Brown ♀ ♀	14.39 ± .037 mm 14.24 ± .037 mm	Black ♂ ♂ Black ♀ ♀	14.08 ± .038 mm 13.95 ± .038 mm	.31 ± .053 mm .29 ± .053 mm	5.8 5.5
Tibia length	Brown ♂ ♂ Brown ♀ ♀	16.30 ± .036 mm 16.02 ± .036 mm	Black ♂ ♂ Black ♀ ♀	16.08 ± .041 mm 15.76 ± .042 mm	.22 ± .055 mm .26 ± .055 mm	4.0 4.7
Body length	Brown ♂ ♂ Brown ♀ ♀ Dilute ♂ ♂ Dilute ♀ ♀	89.9 ± .21 mm 89.0 ± .23 mm 89.9 ± .22 mm 89.0 ± .26 mm	Black ♂ ♂ Black ♀ ♀ Intense ♂ ♂ Intense ♀ ♀	88.4 ± .25 mm 87.5 ± .27 mm 88.5 ± .25 mm 87.6 ± .23 mm	1.5 ± .33 mm 1.5 ± .35 mm 1.4 ± .33 mm 1.4 ± .35 mm	4.5 4.2 4.2 4.0
Tail length	Dilute ♂ ♂ Dilute ♀ ♀	88.2 ± .40 mm 86.0 ± .45 mm	Intense ♂ ♂ Intense ♀ ♀	85.0 ± .33 mm 84.3 ± .37 mm	3.2 ± .52 mm 1.7 ± .58 mm	6.2 2.9
Cranial capacity	No significant differences					

Skull length and skull width show no significant differences.

In humerus length, on the other hand, browns unquestionably surpass blacks. They likewise show significantly greater femur and tibia lengths than do animals with the dominant allelomorph.

Browns significantly exceed blacks in body length. Dilute animals, it will be observed, similarly differ from intense in body length and probably also in tail length.

Cranial capacities exhibit only unimportant differences.

The relations of black to brown back-cross animals in regard to humerus length, body length and adult weight are depicted graphically by frequency polygons in Figs. 1 to 4.

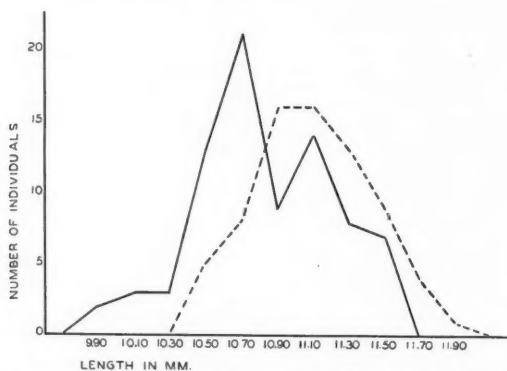


FIG. 1. Humerus length. Back-cross males. Solid line, blacks; broken line, browns.

From the data in Tables II and III, it is evident that several size characters, namely, humerus, femur and tibia lengths, adult weight and body length, are influenced by factors linked with the gene for brown. It also appears that other factors influencing body length and probably tail length are found on the chromosome with dilution. Apparently no special factors affecting skull length, width or cranial capacity are located on any of the "tagged" *musculus* chromosomes.

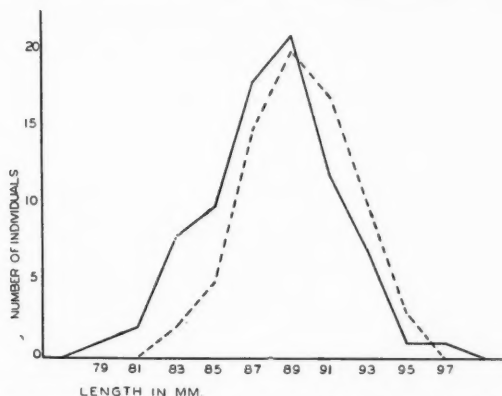


FIG. 2. Body length. Back-cross males. Solid line, blacks; broken line, browns.

Since both femur length and tibia length are markedly influenced by factors, either common or specific, linked with brown, while skull length apparently is not so influenced, the two leg bone lengths should prove to be more closely correlated than is either with skull length. The coefficients of correlation given on page 510 bear out this assumption.

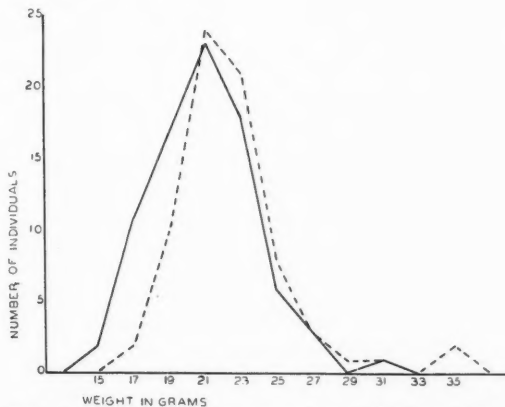


FIG. 3. 181st day weight. Back-cross males. Solid line, blacks; broken line, browns.

	Femur length— Tibia length	Femur length— Skull length	Difference	Difference P. E.
Males .....	$r = +.839 \pm .016$	$r = +.689 \pm .029$	$.150 \pm .033$	4.5
Females ...	$r = +.841 \pm .017$	$r = +.678 \pm .031$	$.163 \pm .035$	4.7

A peculiar situation is revealed in the comparison of agouti and non-agouti: Mice with the former character, which is a dominant and comes into the cross with a chromosome from the smaller species, tend to exceed non-agouti in size. In no case, however, was this difference great enough to reach significance under our criterion. The agouti gene may have some innate beneficial physiologic effect or perhaps it may be linked with other

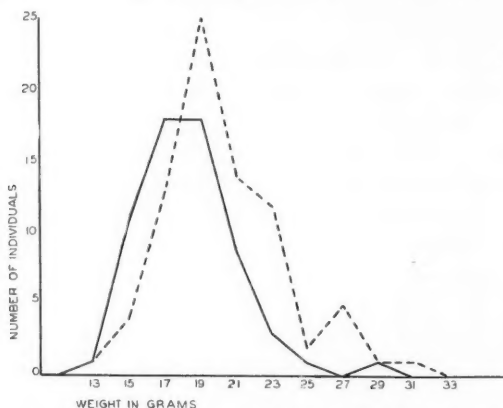


FIG. 4. 181st day weight. Back-cross females. Solid line, blacks; broken line, browns.

advantageous genes. This may give a clue as to the reason for the prevalence of the agouti pattern among wild rodents.

A very small  $F_2$  generation consisting of only 24 animals presents no evidence antagonistic to the findings in the back-cross generation, although of course the numbers are too small to be of any significance. For every adult size character, the average value of the three brown

males and of the three brown females exceeded that of the eight black males and of the ten black females, respectively.

#### SUMMARY

An analysis of the data on the back-cross generation of a mouse interspecific cross between large *Mus musculus*, with three recessive color characters, and small *Mus bactrianus*, with the three dominant allelomorphs, has indubitably shown an association in heredity between factors productive of a large size in several quantitative characters and a recessive qualitative character, brown coat color. Thus, the fact that size in mice is influenced by chromosomal genes can scarcely be questioned any longer. To a lesser extent factors linked with dilution also affect size in certain characters.

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## THE PROBLEM OF UNFRUITFULNESS IN THE CULTIVATED APPLE<sup>1</sup>

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RECENTLY ('29), Wellington, Stout, et al, made this statement concerning the cultivated apple: "Fruit production is complex and dependent upon many factors. . . . The main factors affecting fruit setting may be roughly classified into five categories, namely, meteorological, pathological, nutritional, sexual and agencies effecting pollination." However important the other factors may be, we are concerned here chiefly with the sexual phenomena.

Although Kölreuter, in 1764 (East '29), appears to have been the discoverer of self-sterility in plants, it was not until 1898 that self-sterility (self-unfruitfulness)<sup>2</sup> was discovered in the apple. Waite ('98) of the U. S. Department of Agriculture published an account of his experiments upon barren orchards in Virginia. He concluded that certain varieties of pomaceous fruits were unable to set with their own pollen but that cross-pollination was effective in most cases.

Barring, then, unfruitfulness, due to one or more of the causes other than sexual, the problem that Waite pre-

<sup>1</sup> Acknowledgment is due Dr. O. E. White, under whose direction this work was done while the writer was a Blandy Fellow at The Blandy Experimental Farm and a student at the Miller School of Biology, University of Virginia.

<sup>2</sup> The terms self-fruitful and self-unfruitful have recently taken the place of self-fertile and self-sterile, respectively, in correct horticultural usage. "Chittenden ('14) recalls that self-fertile in its restricted sense implies that viable seed is produced, while in a wider sense, and one that concerns the fruit grower, it means that the pericarp or fleshy envelope of the fruit is formed. There may or may not be any seeds enclosed within it. He proposes, therefore, the term of self-fruitful instead of self-fertile for this latter class, restricting the term self-fertile only to the cross where seed is produced. With this terminology, a fruit tree may at the same time be self-fruitful and self-sterile, or self-fruitful and self-fertile." Quotation from Einset ('30).

sented to horticulturists and later to geneticists was to find which apple varieties were self-fruitful and in which varieties cross-pollination was necessary.

Since then, the problem has been worked at diligently, and although Waite is undoubtedly correct in several cases, a solution to the problem does not seem much nearer now than it did then. The statement made by Fletcher (1900) seems to be as appropriate now as it was thirty years ago, "Self-sterility (self-unfruitfulness) is not a constant character with any variety. It is influenced by conditions under which the tree is grown. . . . No one can separate varieties into two definite classes which are self-sterile. The problem of self-sterility is as much a study of conditions as of varieties. We can set no limits; we can only indicate tendencies."<sup>3</sup>

East ('29) sums up the present position thus: "The situation appears to be that numerous varieties of apples and pears are self-sterile (self-unfruitful)<sup>4</sup> under certain climatic conditions, but are self-fertile under other conditions. . . . The most disturbing phenomenon from the horticultural point of view, however, is the fact that self-sterile varieties ordinarily needing to be crossed with compatible sorts, if merchantable crops are to be produced, sometimes will produce excellent crops when the trees are grown in isolated blocks."

The following table made by Murneek et al ('30) which is an excellent summary of the literature for some of the most important varieties, shows clearly the inconsistency and confusion arising from the results.

The above table is made from the separate works of twenty-five investigators and includes eighteen varieties. Of the 115 accounts on these varieties, only 12 show the necessary 5 per cent. set for a commercial yield. Contrast the accounts of Vincent of Idaho on Yellow Transparent (33.6 per cent.) self-fruitful, with Auchter's of Maryland and Morris' of Washington reports of 0.0 per

<sup>3</sup> From Murneek, et al ('30).

<sup>4</sup> Brackets are mine.

TABLE I  
RANGE OF SELF-FRUITFULNESS OF SOME IMPORTANT VARIETIES OF APPLES

Variety	Investigator	Locality	Number of blossoms considered	Percentage of blossoms set
Arkansas	Lewis and Vincent ('09)	Oregon	?	0.0
"	Auchter ('21)	Maryland	1,909	0.0
"	Auchter and Schrader ('25)	Maryland	543 (s) <sup>5</sup>	0.0
"	Knowlton ('27)	Maryland	500 (s)	0.0
Arkansas, black	Lewis and Vincent	West Virginia	230 (s)	0.0
"	Vincent ('20)	Oregon	?	0.0
"	Auchter	Idaho	448	0.0
"	Auchter	Maryland	2,620	0.0
"	Luce and Morris ('28)	Maryland	228 (s)	0.0
Ben Davis	Lewis and Vincent	Washington	118 (s)	0.0
"	Wicks ('18)	Oregon	?	3.0
"	Gowen ('20)	Arkansas	472 (s)	2.3
"	Vincent	Maine	339	0.0
"	Morris ('21)	Idaho	708	1.2
"	Sax ('22)	Washington	509	0.2
Delicious	Vincent	Maine	1,695	0.4
"	Dorsey ('21)	Idaho	231	0.0
"	Crandall ('22)	Minnesota	73 (s)	0.7
"	Morris	Illinois	?	0.0
"	Whitehouse and Auchter ('26)	Washington	530	0.0
"	Hovlett ('27)	Maryland	687 (s)	0.0
"	Overholser ('27)	Ohio	200 (s)	0.5
"	Luce and Morris	California	426 (s)	0.0
"	Marshall, et al ('29)	Washington	263 (s)	0.0
Duchess	Lewis and Vincent	Michigan	564 (s)	0.0
"	Chittenden ('14)	Oregon	?	5.0
"		England	343	0.3

<sup>5</sup> Covered and selfed; other figures for covered only.

TABLE I—(Continued)

Variety	Investigator	Locality	Number of blossoms considered	Percentage of blossoms set
Duchess	Logsdall ('17)	Ontario	479	0.0
"	Vincent	Idaho	381	19.0
"	Dorsey	Minnesota	271	0.0
"	Morris	Washington	253	11.5
"	Crandall	Illinois	?	0.0
"	Macoun ('22)	Canada	530	11.5
"	Florin ('27)	Sweden	513 (s)	0.0
Early Harvest	Marshall, et al	Michigan	2,162 (s)	0.0
"	Powell ('02)	Delaware	408	5.9
"	Gowen	Maine	13	0.0
"	Vincent	Idaho	152	1.3
"	Crandall	Illinois	?	0.0
Gano	Lewis and Vincent	Oregon	?	0.0
"	Logsdall	Ontario	318	0.0
"	Vincent	Idaho	668	3.6
"	Auchter	Maryland	1,173	0.1
"	Auchter	Maryland	607 (s)	0.5
Golden Delicious	Howlett	Ohio	276 (s)	0.0
"	Knowlton	West Virginia	213 (s)	1.0
Grimes	Powell	Delaware	135	0.0
"	Lewis and Vincent	Oregon	?	14.0
"	Sutton ('18)	England	36 (s)	0.0
"	Wicks	Arkansas	442 (s)	8.0
"	Vincent	Idaho	10,765	2.2
"	Auchter	Maryland	661	1.7
"	Auchter	Maryland	662 (s)	0.1
"	Morris	Washington	2,484	1.5
"	Macoun	Canada	24	0.0
"	Keil ('23)	Ohio	720 (s)	0.0

TABLE I—(Continued)

Variety	Investigator	Locality	Number of blossoms considered	Percentage of blossoms set
Grimes	Howlett	Ohio	148 (s)	0.7
"	Marshall, et al.	Michigan	670 (s)	0.3
Jonathan	Lewis and Vincent	Oregon	?	0.0
"	Wicks	Arkansas	452 (s)	3.8
"	Vincent	Idaho	19,081	2.9
"	Dorsey	Minnesota	188 (s)	2.1
"	Morris	Washington	504	0.0
"	Howlett	Ohio	174 (s)	0.0
"	Overholser	California	600 (s)	0.4
"	Luce and Morris	Washington	282 (s)	3.5
"	Marshall, et al.	Michigan	535 (s)	0.7
"	Vincent	Idaho	605	0.5
King David	Dorsey	Minnesota	195 (s)	0.0
"	Lewis and Vincent	Oregon	?	0.0
Ralls	Keil	Ohio	720 (s)	0.0
Rome	Lewis and Vincent	Oregon	?	0.0
"	Alderman ('17)	West Virginia	16,826 (s)	1.0
"	Logsdail	Ontario	166	0.0
"	Vincent	Idaho	10,326	4.5
"	Keil	Ohio	720 (s)	0.0
"	Howlett	Ohio	80 (s)	2.5
Stayman	Luce and Morris	Washington	110 (s)	10.0
"	Powell	Delaware	106	0.0
"	Auchter	Maryland	845	0.0
"	Auchter	Maryland	560 (s)	0.0
"	Crandall	Illinois	?	0.0
"	Howlett	Ohio	70 (s)	0.0
"	Knowlton	West Virginia	1,795	1.6
"	Luce and Morris	Washington	216 (s)	0.0
Wealthy	Waugh ('98)	Vermont	28	0.0

TABLE I—(Continued)

Variety	Investigator	Locality	Number of blossoms considered	Percentage of blossoms set
Wealthy	Lewis and Vincent	Oregon	?	0.0
"	Chittenden	England	30	0.0
"	Logsdail	Ontario	172	2.0
"	Vincent	Idaho	351	3.7
"	Aucher	Maryland	1,059	4.5
"	Aucher	Maryland	799 (s)	1.9
"	Morris	Washington	647	0.5
"	Macoun	Canada	125	6.4
"	Keil	Ohio	720 (s)	0.0
"	Hovlett	Ohio	84 (s)	0.0
"	Marshall, et al.	Michigan	658 (s)	0.8
Winesap	Powell	Delaware	300	0.0
"	Lewis and Vincent	Oregon	?	0.0
"	Wicks	Arkansas	500	0.4
"	Vincent	Idaho	365	0.0
"	Morris	Washington	1,096	1.6
"	Crandall	Illinois	?	0.0
"	Luce and Morris	Washington	910 (s)	0.0
Yellow Transparent	Powell	Delaware	363	5.5
"	Lewis and Vincent	Oregon	?	8.0
"	Logsdail	Ontario	605	0.9
"	Vincent	Idaho	107	33.6
"	Aucher	Maryland	514	2.7
"	Aucher	Maryland	42 (s)	0.0
"	Morris	Washington	510	0.0
"	Florin	Sweden	607	1.2
"	Powell	Delaware	134	0.0
York	Lewis and Vincent	Oregon	?	0.0
"	Alderman	West Virginia	21,742 (s)	0.6

cent. The difference in locality can hardly be expected to account for so much variation in results.

Three definite conclusions can be drawn from this table:

(1) Self-pollinated apple trees can not as a rule be depended upon to produce a satisfactory crop.

(2) Some varieties are more self-fruitful than others.

(3) The inconsistency of results indicate that there is some discrepancy in this method of attack and that all the factors that enter into the set of the apple are not accounted for.

Hoping to throw some further light upon this complex subject, the writer during the years 1928-1929, at The Blandy Experimental Farm of the University of Virginia, attempted to find the extent of self-unfruitfulness existing among the different apple varieties at hand.

Following the method in vogue, unopened flowers from the varieties to be used as pollen parents were secured and left covered in a dry place until the anthers dehisced. This pollen was applied with a camel's hair brush to the unopened emasculated flowers of the variety to be used as the female parent. These pollinated flowers were not covered since several experiments both by myself and others (Sax '22) have proved that bees do not visit flowers so treated. Wind pollination is a negligible factor in the apple.

The composite results on self-compatibility for the two years are as follows:

TABLE II

Of 44 self-pollinated	Grimes Golden	flowers 2 set or 4.5 per cent.
" 170 " "	York Imperial	" 5 set or 2.9 per cent.
" 79 " "	Stark's Delicious	" 1 set or 1.2 per cent.
" 41 " "	Stayman's Winesap	" 0 set or 0.0 per cent.
" 39 " "	Winesap	" 0 set or 0.0 per cent.
" 183 " "	Baldwin	" 1 set or 0.5 per cent.
" 55 " "	Ben Davis	" 0 set or 0.0 per cent.

This table except for the results on Baldwin merely increases the range of Table I.

Howlett ('27) of Ohio eliminated experimental error almost entirely in the case of Baldwin, when he enclosed one whole tree under a muslin frame with a hive of bees. From these self-pollinated flowers he received a 5 per cent. set whereas an open pollinated tree nearby gave a 25 per cent. set.

The literature on cross-compatibility is even more confusing and inconsistent than that on self-compatibility. A particular variety may be reported as an effective pollenizer for another particular variety or group of varieties by one investigator and the reverse is found by another worker. However they all agree that the pollen of a variety is generally more effective upon the flowers of some other variety than upon its own.

In Table III are summarized the data from my cross-compatibility tests. These varieties were intercrossed, each with each, but for the sake of brevity and since nothing would be gained from a detailed account, the data are presented chiefly from the standpoint of the pollen parent.

TABLE III

The pollen of:					
Grimes Golden	used in 213 pollinations	gave	9 sets or	4.2 per cent.	
York Imperial	" " 85	" "	15 " "	17.6 per cent.	
Stark's Delicious	" " 138	" "	24 " "	17.4 per cent.	
Stayman's Winesap	" " 203	" "	9 " "	4.4 per cent.	
Ben Davis	" " 131	" "	5 " "	4.5 per cent.	

Except for Grimes Golden the per cent. set was increased greatly by cross-pollinations. My results together with those of more than 100 other investigators prove that cross-pollination *does* increase the fruitfulness of an orchard.

Crane and Lawrence ('29) have said: "Sterility in fruits is of three fundamentally different kinds: (1) *generational sterility*, due to the failure of any of the processes concerned with the normal alternation of generations, namely, development of pollen, embryo sac, em-

bryo and endosperm, and the relations of these with one another and with their parents regardless of the cross made; (2) *morphological sterility*, due to the suppression or abortion of sex organs; (3) *incompatibility*."

#### INCOMPATIBILITY

The above authors, Crane and Lawrence ('29) defined incompatibility thus:

"In this third form of sterility we are not dealing with sterility in the strict sense of the word, as both the ovules and the pollen—or at least a good proportion of them—are functional. The failure to obtain fruits from self- and cross-incompatible pollinations is due to the absence of fertilization, the pollen tubes becoming arrested in the nutrient stylar tissue. On the other hand, in compatible pollinations, although the same pollen and ovules take part, the pollen tubes travel the full length of the style. The male and female nuclei fuse and the fertilized ovary develops into a fruit."

Since Waite's pioneer work on the relative compatibility of pollinations, probably every variety of commercial importance has been tested as to self-compatibility and most of them have been inter-tested as to cross-compatibility.

There are probably a few definite cases of complete physiological self-incompatibility in the apple (examples, Arkansas and Arkansas Black) where the pollen of a variety is not capable of inducing fruit formation in its own ovary.<sup>6</sup>

This being the case it is only natural to expect that there should be cases of physiological cross-incompatibility. However, Florin ('26), Howlett ('27) and others, agree that no definite cases of physiological cross-incompatibility have ever been found.

The work of East and Mangelsdorf ('25 and '26), Lehmann ('26) and Sirks ('26) all of whom have arrived

<sup>6</sup> Crane and Lawrence ('30) seem to be in doubt as to the existence of any cases of complete self-incompatibility. They say: "As far as our investigations go, incompatibility occurs in varying degree but is rarely, if ever, completely expressed in apples as it is in plums and cherries."

independently at fundamentally the same conclusions offers a possible theoretical explanation to this problem. Taking, for example, the work of East and his collaborators on the inheritance of self-sterility in highly homozygous tobacco species, they have found that incompatibility is determined by genetic factors just as are morphological characters. These factors form a multiple series, and in a manner similar to some other Mendelian factors any two of them may be carried by a given plant. Pollen can not function in the style of a plant carrying the same incompatibility factors as the pollen. "Like repels like." Self- and cross-pollinations between individuals with the same genetic constitution with respect to incompatibility factors fail.

Following the terminology (Fig. 1) of East and Mangelsdorf ('25) as given by Crane and Lawrence ('29) an individual with the constitution S 1 S 2 can not be fer-

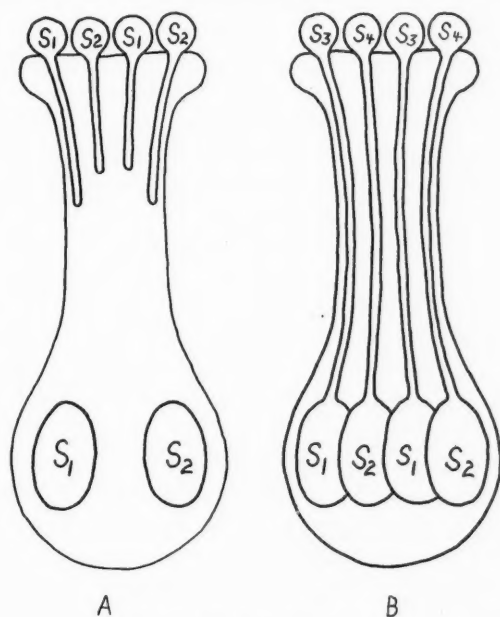


FIG. 1. Explanation in text.

tilized by S 1 or S 2 pollen (Fig. 1A). However, in the cross S 1 S 2 x S 3 S 4 both S 3 and S 4 can effect fertilization (Fig. 1B).

If the work on tobacco holds equally well for apples then the failure to find cases of physiological cross-incompatibility might be explained by the interaction of these sterility factors. Though varieties differ markedly in respect to heterozygosity, some even practically breeding true, the chances are strong that the same factors for sterility will be found in both the male and female gametes on the same plant and hence repel each other. In the case of cross-pollination, even though both parents have factors for sterility, the chances are greater that compatible gametes will have a chance to function. *Cross-pollination* has been proved to increase the fruitfulness of an orchard.

By the interaction of these sterility factors, not only should we expect cross-pollination to bring together favorable gametes but also, due to the highly heterozygous condition of the apple, the gametes produced will be of numerous genotypes and out of a large number of pollen grains there should be some that would be functional on their own ovules. If, then, the stigmas are sufficiently covered with the pollen, even from the same flower, the chances for fertilization are greatly increased. A case in point is the Grimes Golden. I have observed that the styles of this variety which are longer than the stamens bend down as if through some attraction and cover their stigmatic surfaces with pollen from the anthers. As should be expected this variety, although an early bloomer, is a heavy bearer. Most of the self-compatibility tests that have been carried out on this variety have found it self-sterile. Nevertheless, this is one of the most extensively cultivated varieties in the United States and is seldom if ever barren.

Further, as is pointed out in Table IV, "triploid" varieties produce notoriously poor pollen, and neglecting incompatibility the "diploids" as a rule would be more

effective as pollinizers in the field than the "triploids." Crane and Lawrence ('30), however, have shown that "the 'triploid' combinations have in our experiments given even slightly better results in the production of fruits than the 'diploids.'" They account for this in a manner somewhat similar to the case of Grimes above. They say: "Since incompatibility is due to lack of genetic differentiation, the good results obtained from the 'triploids' are probably due to a greater variety in the gametic output of 'triploid' than of 'diploid' varieties, thereby providing a greater chance of compatible combinations." "Triploid" varieties have been shown to be productive in the field, *i.e.*, Bramley's Seedling, Baldwin and Gravenstein. Crane and Lawrence ('30) point out the fact that Bramley's Seedling is the most widely cultivated variety in England. They further add: "In apples, degrees of incompatibility are common even in the so-called 'diploid' varieties; this may be attributed to their secondary polyploid complement (explained below), which involves a polysomic condition of the incompatibility factors. Every chromosome and hence its factors may be represented two or three times in the gametophyte which provides a basis for greater variation in the number of possible combinations of a given factor."

#### GENERATIONAL STERILITY

As defined by Crane and Lawrence ('29) this form of sterility is due to the failure of any of the processes concerned with the normal alternations of generations; namely development of pollen, etc.

For several years it has been noted that the pollen of certain varieties was, as a rule, functional in producing fruit with most any other variety, if not on the stigma of its own flowers. The results set forth in Table III show clearly that Stark's Delicious pollen is more useful than Stayman's Winesap, for example. Because of this variation in the effectiveness of pollen, it is highly important to know the ability of the pollen of the different

varieties to germinate. I tested the pollen from the varieties that were used in pollination tests on a 5 per cent. sugar medium and found that less than 30 per cent. of the pollen grains of Stayman's Winesap, Baldwin (triploid) and Ben Davis germinated. The pollen of York and Grimes germinated as high as 70 per cent. while that of Stark's Delicious was as high as 90 per cent. Referring to Table III it can be seen that the per cent. germination is correlated with the value of a variety as a pollinizer.

Germination tests have received much attention recently.

Following is a table from Crane and Lawrence ('30).

TABLE IV

Variety	Chromosome numbers (3n)				Per cent. pollen germination		
	Rybin	Kobel	Nebel	Darlington and Moffett	Kobel	Kvaale	Florin
Baldwin .....	48-49	51	51	11.0	12.3	0.0-30.0	
Belle de Boskoop .....	ca. 46	51	13.0	.....	0.0-30.0		
Blenheim Orange .....	51	51	.....	.....	0.0-30.0		
Bohnappel .....	46-49	.....	10.0	.....	.....		
Bramley's Seedling .....	.....	.....	51	.....	20.9	0.0-30.0	
Crimson Bramley .....	.....	.....	51	.....	.....		
Damason Reinette .....	45-47	.....	23.0	.....	.....		
Genet Moyle .....	.....	.....	51	.....	.....		
Gravenstein .....	45-46	51	7.0	13.0	0.0-30.0		
Gravenstein (7 clonal varieties) .....	.....	51	.....	.....	.....		
Harbert's Reinette .....	45	.....	16.0	.....	.....		
Jaques Lebel .....	49-51	.....	13.0	.....	.....		
Reinette du Canada .....	51	38-40	51	4.0	.....	0.0-30.0	
Ribston Pippin .....	42	51	51	21.4	0.0-30.0		
Roter Eiserapfel .....	47	.....	.....	.....	.....		
Stäffner Rosenapfel .....	48-49	.....	25.0	.....	0.0-30.0		
Warner's King .....	42	.....	27.0	14.8	0.0-30.0		
Winter Zitronenapfel .....	48-49	.....	21.0	.....	0.0-30.0		
Lane's Prince Albert (1) .....	.....	.....	34 <sup>7</sup>	57.6	70.0		
Lane's Prince Albert (2) .....	.....	51	.....	.....	.....		

<sup>7</sup> 2n.

From this table, which contains only "triploids," except for one case, Lane's Prince Albert, it is seen that all the "triploids" germinated less than 30 per cent. The authors have said, "Although there is considerable variation in the proportion of good pollen among the known 'diploids,' the worst 'diploid' has a much higher proportion than the best 'triploid.'"

However, as pointed out above, even though the pollen from these "triploid" varieties contains a large proportion of non-germinating grains, due to the variation among them they are in most cases valuable as pollenizers.

In some cases the poor germination ability of the pollen has been accounted for from a cytological standpoint. Shoemaker ('25) followed the development of apple pollen from the pollen mother cell stage through to mature pollen. He found that in those varieties, such as Stayman's Winesap, where the pollen is consistently poor, that the reduction division is not regular and a number of pollen grains arise which are unbalanced from the standpoint of chromosomal content and are not capable of germination.

As far as the writer knows, no work has been done on irregularities in development and function of the ovules, nevertheless, no doubt what is said of the pollen grains is probably also true of the female element.

#### PARTHENOCARPY

To further complicate matters we find that in the apple fertilization apparently supplies the requisite initial stimulus to fruit development and that even one seed need not be the result. Again quoting Crane and Lawrence ('30): "In the apple a single seed is often sufficient for the development of the fruit, and even this seed may be imperfect. This approaches parthenocarp and renders fruit production still less dependent on the formation of seeds. In some varieties of apples entirely seedless fruits are not uncommon." The theory set forth above that the productiveness of "triploid" varie-

ties was due to incompatibility factors being overwhelmed by the increased gametic variation is not strengthened by the fact that Crane and Lawrence ('29) have found only 1.3 good seed per fruit in open pollinated Bramley's Seedling. It is the opinion of the writer that parthenocarpy has not received the attention it should have.

#### CHROMOSOME NUMBER AND ITS SIGNIFICANCE

According to Crane and Lawrence ('30), 48 varieties have been found to be "diploid" ( $2n=34$ ) and 24 have been found "triploid" ( $3n=51$ ). Hence with an apparent basic number of 17 all the cultivated varieties are orthoploid. Seedlings with an intermediate number aneuploid) do arise but have been found by Darlington and Moffett ('30) to be of feeble growth and hence would be useless in cultivation.

The "haploid" number of seventeen is an anomaly in the Rosaceae, where seven and eight have been generally found. Darlington and Moffett ('30), in a brilliant contribution, bring forth convincing evidence to support their conclusion that the primary chromosome complement of *Pyrus* is seven and that in the "diploid" *Pyrus* there is a long type of chromosome which is represented four times, while in "triploid" varieties this long chromosome is represented six times. In "diploid" material, morphologically, the 34 chromosomes may be further associated (called multiple association) into seven groups, four quadrivalents and three sexivalents. "*Pyrus* is therefore shown by its chromosome behavior to be functionally a 'diploid' while historically it is quadruply tetrasomic and trebly hexasomic." Further evidence of a primary number of seven is gained from the fact that natural seedlings of "triploid" varieties most frequently have a chromosome number approximating  $2n+7$ . The genetical complexity of *Pyrus* which the present paper has tried to emphasize is cited as additional evidence.

These findings are both significant and practical, as the authors point out, because of the fact that the balanced condition, as found in the majority of the Rosaceae, has been tested by the rigors of natural selection, while the unbalanced *Pyrus* has yet to put its destiny in the hands of chance.

They say: "Since evolution proceeds largely, if not entirely, by changes in the balance of the hereditary materials, it is plausible that this method of change, the extreme of discontinuity, will in one case out of a very large number yield (at least with later selection) a product as vigorous and as fertile as its antecedents." "It must be remembered that the difference between balance and unbalance is merely the difference between a system that has been tested by natural selection and one that has not. The difference therefore depends upon chances."

I should like to point out the fact, however, that there is little chance of change in the established varieties, due to their method of propagation, and that progress from the above source depends mainly upon the breeding and selection of seedlings.

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THE OPAH OR MOONFISH, *LAMPRIS LUNA*,  
ON THE COASTS OF CALIFORNIA  
AND OF HAWAII

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I HAVE previously published two faunal articles on this rare and interesting fish. The earlier (1926) made known its first recorded taking in the Gulf of Mexico. The second (1930) listed the capture of two new (and three old) specimens on our eastern coast and gave a figure of the finely mounted skin of one of these. In this article I also synthesized the natural history of the fish so far as it could be gathered from the widely scattered literature.

In the present article I plan to bring together the scattered published accounts of its occurrence on the Pacific Coast and in Hawaii and to add to these a considerable amount of unpublished data which has come to my hand. Acknowledgment will be made to my informants in the body of the text.

THE OPAH IN CALIFORNIA WATERS

The published records of the occurrence of this fish on the coast of California are very few and very lacking in details. Thus Jordan and Evermann say in 1896, "At Monterey and other places in California. Our specimen is from Monterey." This fish is presumably that also recorded by Evermann the same year (1896). He did not see this specimen (for which no size is recorded) but he easily identified it from the description in a letter sent him. His informant seems to have seen several specimens.

David Starr Jordan in a much later book (1905) said that "the specimen studied by the writer came ashore at Monterey in an injured condition." This possibly is the fish referred to by Jordan and Evermann (1896), and it

may be the one recorded by Evermann (1896) (but on this latter point Evermann writes me, "My impression is that they were two entirely different specimens"). Jordan in the same book (1905) speaks of "another taken at San Pedro Pt. (near San Francisco)."

Very indefinite are Jordan and Starks (1907) who merely say, "Occasionally taken about Santa Catalina. Two stuffed specimens were seen." Later Starks and Morris (1907) say that "Mrs. Andrews, of San Diego, has a painting of this species from a specimen caught in the vicinity. . . . There are two skins of the Opah at Avalon." Next C. F. Holder (1912) states that four or five had been caught near Santa Catalina. He gives two good figures (evidently made from photographs) of the fish (presumably mounted specimens) but nowhere gives any dates of capture, nor any pertinent data as to sizes ("attains a weight of 70 pounds"). This is greatly to be regretted since he probably had practically first-hand knowledge of these specimens.

A more definite note is that of Thompson (1924) on a specimen brought to the San Pedro market in 1924. It was caught about the middle of May, in a mackerel net about one mile off Point Fermin. It weighed about 50 pounds.

The latest published record from the Pacific coast known to me is dated 1929. This (Anon. 1929) is an absurdly written popular (?) account of a 97-pound fish taken in a net off San Pedro. Its "diameter" (dorsio-ventral) is noted as about 3 feet (whether over body only or over dorsal and ventral fins is not stated, but probably the latter) and its thickness as 2.5 inches (which must be an error).

To these few published records of the opah on the southern coast of California are now to be added a considerable number of unpublished ones. First are two which give numerous details, which can be set out in tabulated form. The first is a fish seen and carefully described on October 22, 1918, by Elmer Higgins, of the

U. S. Bureau of Fisheries, who writes of the opah in general that "I distinctly recall seeing several specimens of *Lampris* on the Southern California coast, usually taken in sardine nets which fish in less than 10 fathoms of the surface."

The data referred to were left by Higgins at the California State Fisheries Laboratory at Terminal Island and were copied and preserved by Thompson. Along with these data there is preserved in the same archives the detailed record of another *Lampris* taken off San Pedro and brought to the market on May 12, 1924. For transcripts of these accounts I am indebted to the kindness of Mrs. Genevieve Corwin Wheeler, librarian of the laboratory. These data and those for the Massachusetts fish described in my previous paper are set out in tabulated form below that comparison may be made between the two Pacific fish, and between them and the Atlantic specimen.

COMPARATIVE DATA FOR THREE SPECIMENS OF *Lampris luna*

Measurements in inches	Length, total	Length, standard	Weight, lbs.	Depth	Head, length	Maxillary, length	Diameter of eye	Dorsal, height	Dorsal rays	Pectoral, length	Pectoral rays	Anal rays	Pelvic rays	Depth, caudal peduncle
San Pedro 1918.....	36	33.5		21.8	11.3	3.6	1.9	9.4	48	9.9	24	42	13	
San Pedro 1924.....	36.5		46	20	10	3.6	2	10	49	8.5		33	15	2.5
Hyannis, Mass., 1928.....	31.7	27.1	32	16.7	8.5	2.8	2	10.1	49	8.2	21		14	2

In the table there is but one marked discrepancy, that of the divergent count of anal rays. The commonly accepted count (Jordan and Evermann, 1896) is 38 to 41. Presumably the count of 33 is an error. Additional data for which space is lacking in the table are for the 1918 fish: interorbital space 124 mm (4.9 in.); length of ven-

tral, 266 mm (10.5 in.); pores (*i.e.*, scales?) in lateral line about 80, and in the Massachusetts fish about 86; the caudal rays were 30. Additional data for the 1924 fish are: length of snout, 109 mm (4.3 in.); diameter of pupil 23 mm (0.9 in.).

I will now present certain very fragmentary data for eight other specimens taken around Catalina. These data while very imperfect at any rate indicate the relative abundance of the fish in these waters. All came to me through the kindness of the well-known angler, Mr. Andy Martin, of Beverly Hills, California. None of these data (covering about 30 years) have been previously published. The fish referred to have been mounted, and Mr. Martin has seen every specimen save one. Notice of these will now be set out.

There hangs in the Tuna Club at Avalon, Santa Catalina, a mounted opah measuring 3 feet, 6 inches from tip to tip, and 2 feet, 11 inches in depth (over fins?). Its weight is estimated at about 60 pounds. The fish was taken about 1900. At Avalon, there is another on the wall of Joe Cameron's restaurant, and yet another is on display in MacRae's fishing tackle store. For neither of these latter have I been able to get any measurements or dates of capture.

Two others are on display in large stores in Los Angeles. I have had no answer to my letter concerning the one in the Tuft-Lyons Arms Company. However, the B. H. Dyas Company writes that their specimen is 43 inches (1,092 mm) from tip to tip. The greatest depth is 25 in. (635 mm) and dorsal fin is 8.5 in. (210 mm) high. The dates of capture for these fish can not be ascertained, but both were taken near Catalina.

Three Catalina fish have been mounted by Mrs. C. B. Parker of Avalon, whose letter corroborates Mr. Martin, and have been taken elsewhere. One is in Des Moines, Iowa, and two are the property of Mr. William Wrigley, Jr., of Chicago. No data are available for that at the Chicago Baseball Park, but Mr. Martin has seen and

measured that in the tower room of the Wrigley Building. This mounted fish is 1,270 mm (50 in.) long between perpendiculars; 720 mm (30 in.) deep, and the spread of the tail is 350 mm (14 in.). The depth at the hinder edge of the operculum is 508 mm (20 in.). From the tip of the snout to the center of the eyes is 203 mm (8 in.) and to the hinder edge of the operculum 380 mm (15 in.). The dorsal is 240 mm (9.5 in.) high and 508 mm (20 in.) long. The length of the pectoral fin is 267 mm (10.5 in.), that of the pelvic 267 mm (10.5 in.) and the length of the anal 356 mm (14 in.). The weight is given on the tag as 160 lbs. The fish was taken by market fishermen at Emerald Bay, Catalina Island, in 1924.

In my previous paper it was shown that the opah of our north Atlantic coast is a deep-water fish and is taken ordinarily on trawl hooks. So far as the records go, on the Pacific coast it is taken only on, at, or near the surface, either in nets or with the gaff. Holder wrote in 1912, "It is said that one was taken off San Clemente with rod and reel." This statement has often been repeated and Mr. Wrigley's specimen is also said to have been hooked, but the investigations of Mr. Martin and the officials of the Tuna Club prove these accounts to be erroneous. None on the southern California coast has ever been taken on the hook so far as records go. The universal explanation of their capture at the surface at Santa Catalina is that they get into cold water and become more or less disabled, come to the surface and float about helplessly or feebly swim into bays where the water is warmer—in any case are taken at the surface either in nets or with the gaff.

In my article on the occurrence of the opah on our north Atlantic coast I was able to account for five specimens, or taking into consideration the one on the west coast of Florida, a total of six fish. When one recalls the intensity of fishing operations from Newfoundland to Nantucket, and the length of time they have been carried on, one must draw the conclusion that the fish is very

rare in those waters. Turning, however, to California, there are listed herein six published accounts and two scientific records of its occurrence on the southern coast of California. Of these eight records, two fish were taken at Monterey, one at San Diego and five at San Pedro. There are definite records of eight mounted specimens taken from Catalina waters. There are then sixteen definite records, plus a number of indefinite ones (possibly in some cases duplicates of others) of the occurrence of *Lampris luna* in the waters of southern California. The contrast between these sixteen records for our Pacific coast and the six for our Atlantic and Gulf waters is certainly a remarkable one. Further, since five of these latter were taken between Newfoundland and Cape Cod, that is to say in our northern and colder Atlantic waters, it is particularly notable that on our Pacific coast there are no records for the Washington and Oregon coasts, for the colder Pacific waters.

#### A FOSSIL MOONFISH FROM SOUTHERN CALIFORNIA

Since the moonfish is now found more abundantly in California waters than elsewhere on our coasts, it is interesting to note that it was found there in geologic times also. Jordan has described (1920) a fossil moonfish three feet long by about two feet deep from beds of Miocene diatoms at Lompoc, Santa Barbara County, California. He concludes his account with the following statement: "The specimen is one of great interest as showing the antiquity of one of the most singular of all living bony fishes, and incidentally with other associated forms, the relative age of the present fish fauna of California."

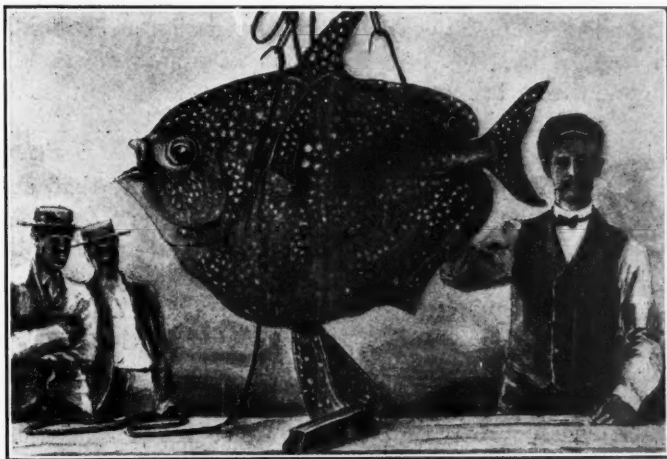
However, Jordan refers to this fish as "a second species of moonfish." Then he continues, "Two smaller specimens, apparently of the same species, but lacking the head and shoulder girdle, had been previously found at Lompoc." A very indefinite reference led me to find

that Jordan and J. Z. Gilbert in 1919 had, from a study of a portion of the vertebrae only, described these fish as *Diatomoeca zatima* of the family Pleuronectidae. Furthermore this identification is repeated by these same authors in a later publication (1920).

However, Jordan in the *Scientific Monthly* article concludes that these vertebrae, previously determined as pleuronectid, actually belong to *Lampris zatima*. His figure of the nearly complete skeleton leads to the belief that this is correctly identified as a *Lampris*.

*Lampris luna* IN HAWAIIAN WATERS

This fish is also found in the waters around our island possession. The earliest reference (Jordan, 1905, vol. I, p. 323, fig. 199) is to the giant of the tribe, a specimen in the Honolulu market said to have weighed 317.5 pounds. This figure is made from a photograph sent in by Mr. E. L. Berndt, who captured the fish near Honolulu. Unfortunately Jordan does not give its dimensions or state



—After Jordan, 1905

FIG. 1. An Opah, *Lampris luna*, photographed by E. L. Berndt in the Honolulu Fish Market. Weight listed as 317.5 pounds.

how it was taken. Since this is the record opah of the world, and since it gives the form and markings in photographic reproduction, it is copied here as Fig. 1 to give it a wider distribution than can be had in Dr. Jordan's book.

The next Hawaiian record I find is a very indefinite and unsatisfactory one from Jordan and Evermann (1905), who merely state that "Mr. Berndt sends a photograph of a specimen of this species, weighing 176 pounds, taken off Honolulu." One can not but wonder if this is not the same fish as that referred to above. Had the statements included the dimensions, the matter would have been effectually settled.

Next, Jordan, in the article (1920) on the fossil form previously referred to, figures a beautiful cast of a *Lampris* weighing 100 pounds taken near Honolulu. Whether this is in the Bishop Museum, Honolulu, can not be said. Two years later Jordan and Jordan (1922) in their "Fishes of Hawaii" write that: "An example, six feet long, was once taken at Honolulu. It weighed 217 pounds." This is evidently a repercussion of Jordan's statement in 1905, but inspection of his photographic figure with a tall man standing beside the fish will make it clear that this specimen was not six feet long. These accounts seem to be very much confused.

Finally Jordan and Jordan (1922, p. 29) say that, according to the Honolulu *Star-Bulletin*, another *Lampris* was taken in 1922 about 13 miles west of Oahu at a depth of 1,200 feet. Dr. S. C. Ball, of Yale University, who was at that time connected with the Bishop Museum, writes me that he weighed this fish and that it tipped the scales at 117 pounds. This is the fish referred to by Fowler (1928) as being taken by Japanese fishermen off Waianea beach, Oahu, March 10, 1922. It measured 1,185 mm (46.7 in.).

What is the maximum size of *Lampris luna* can only be conjectured. Jordan says, on what authority I can not

state, that it attains "a length of 6 feet and a weight of 500 or 600 pounds." But it can be stated on the authority of Baikie (1853) that one captured at Sandey, Orkney Islands, was "nearly six feet" long. Now the 317.5-pound specimen figured by Jordan is certainly not that long, and one can only conjecture how much a 6-foot specimen of *Lampris luna* would weigh.

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## MCDUGALL'S LAMARCKIAN EXPERIMENT

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A REVOLUTIONARY and important conclusion has been reached on the basis of experimental results by the eminent psychologist, William McDougall.<sup>1</sup> As a result of training rats to perform a specific task for many generations, this investigator claims to have induced inheritance of a specific modification in their behavior. If his data and inferences become established, McDougall will have inaugurated a revolution in genetics even more far-reaching than the one inaugurated by Muller when he increased the rate of mutation in *Drosophila* by means of x-rays. For not only does McDougall claim to have induced mutations, but he claims, in effect, to have induced a progressive series of adaptive mutations. Moreover, a specific treatment was designed to produce just this particular series of mutations and the inference is that any one of many series of mutations might similarly have been produced by appropriate experimental procedures.

McDougall has frequently invited criticism and discussion of his work and, in view of the very great importance of the issue, this seems highly desirable. With this in mind I shall bring together here the impressions the work has made on some other investigators and on myself.

Professor F. A. E. Crew discussed McDougall's work in the *Eugenics Review* for April, 1930. He is of opinion that the work is free from the commoner errors that vitiate most work on the Lamarckian hypothesis, but that it is subject to one very serious flaw: namely, the possi-

<sup>1</sup> McDougall, Wm., "An Experiment for the Testing of the Hypothesis of Lamarck," *The British Journal of Psychology* (General Section), xvii, part 4, April, 1927; "Second Report on a Lamarckian Experiment," *ibid.*, xx, part 3, January, 1930.

bility that the parent rats, which have been trained to the task, communicate to their young something concerning the experience they have been through and that this tradition is built up more and more effectively from generation to generation. So that one deals here not with genetical inheritance but with "social" inheritance.

Professor Crew supports his criticism by an account of similar "social" inheritance among birds. This support for his criticism is really the important thing, because McDougall has already considered and rejected nearly all, if not all, serious criticisms that could be suggested. To Crew's evidence for social inheritance I shall add evidence for two other criticisms that have also been considered and rejected by McDougall. The first of these is the likelihood of inadvertent selection (a criticism so frequently made against work of this sort); the second, and more important, is the possibility that the "improvement" in learning in successive trained generations is an expression not of genetic differences but of differences in the strength of the electric shock used to train the rats.

It will be recalled that the task the rats were trained to perform was to escape from a water tank by means of an unilluminated gangway and invariably to refuse to escape by means of an alternative illuminated one. The method used to discourage the rats from using the illuminated gangway was to electrify it so that each time a rat attempted to use it, the rat would get a shock. Twenty-three generations of rats were trained by means of such shocks to avoid the illuminated gangway. In the later generations the rats required very much less training—that is, fewer shocks—to learn this than they had required in the earlier generations. Although the experiment is still in progress and the published data are merely preliminary reports, McDougall feels that they can only be interpreted as evidences of Lamarckian transmission.

The shocking apparatus was such that, according to McDougall, there was unavoidable variation in the

strength of the primary current, the behavior of the interruptor, and the kind of contact made by the rats. In order to discover whether the difference in mean number of shocks necessary to train the experimental and the control groups of rats might be due to these variations in the strength of the shock, one of McDougall's associates, Dr. Rhine, used three definitely different intensities of shock in attempts to train representatives of the last (23rd) generation of trained rats and of a "control" group (ancestors trained for only four generations). Dr. Rhine found in both groups that the heavier shocks trained more quickly than the lighter shocks. Nevertheless, the rats from the last (23rd) generation of training made a very much better record even when trained by application of light shocks than did rats of the "control" group when trained by application of a heavy shock. In view of the fact that McDougall believes all his shocks to have fallen within the range of medium to heavy, he concludes that variations in the shocks as he applied them could not be very important in determining the mean difference between the "control" rats and the experimental rats. This conclusion seems sound.

These data may be viewed, however, in a somewhat different way. Instead of comparing the records made by the last trained generation with the records of the "controls," the records of the last trained generation when trained by means of the three definitely different intensities of shock by Dr. Rhine may be compared with the records of the same generation when trained by McDougall. Dr. Rhine's results are given in terms of number of days of training required before learning; Professor McDougall's results are given in terms of number of errors made before learning. Either of these data can be converted into the terms of the other with a fair degree of correctness on the assumption (justified by their data) that, before learning, the rats go, on the average, as frequently to the wrong gangway as to the right one. It is known that each rat gets six trials per day. In

Table 1, I have converted Dr. Rhine's data so as to be comparable to the data of McDougall and his assistant, Mr. Heck.

TABLE 1  
COMPARISON OF THE RESULTS OF DIFFERENT INVESTIGATORS USING  
DIFFERENT INTENSITIES OF SHOCK

Investigator	Dose	Generation	Number of rats	Average number of errors per rat
McDougall	Heavy to medium	23	26	25
Rhine	Heavy	23	4	27
Rhine	Medium	23	4	54
Rhine	Light	23	4	77
Heck	?	14, 15, 16	25	75

Dr. Rhine's data, given in terms of number of days of training required to teach the rats, have been converted by the present author (as explained in the text) into terms of number of errors made by the rats before learning.

This table shows that Dr. Rhine found the mean number of errors (27) made by the rats when trained with heavy shocks to be only half as great as the mean (54) for the same generation of rats when they were trained with medium shocks. Furthermore, the mean found by McDougall (25) is very close to the mean found by Rhine when using the heavy shocks. These two comparisons indicate that McDougall was working at the upper limit of his shocking intensity on this generation and that, had he worked at his lower limit (medium shocks), he probably would have obtained a mean of about 54 errors. A mean of this magnitude is greater than any mean reported for the last seven of the ten generations included in the 1930 paper, with the single exception of the 18th generation with a mean of 62 errors.

I group together the records of the last seven generations to contrast them with the records of the three pre-

ceding generations, for three reasons: First, there is an abrupt change in the records as one passes from the earlier to the later group. The average number of errors for the first three generations (generations 14, 15, and 16) are 80, 70, and 73, respectively. For the next seven generations (with the exception of the 20th generation, for which data are not reported) the averages are 46, 62, 47, 37, 36, and 25, respectively. Secondly, the records of the earlier group of generations do not fall within the range obtained by Dr. Rhine with his medium to heavy shocks, although the records of the later group of generations do (with the single slight exception of the 18th generation, as noted above). Third, the earlier group of generations was trained not by McDougall, but by an assistant, Mr. Heck; the later group of generations was trained by McDougall himself.

There is much to indicate that the marked difference between the records of the generations trained by Mr. Heck and the records of those trained by Professor McDougall may be due not to genetic differences, but to differences in the intensity of shocking. McDougall states that all his own shocks fell within the range medium to heavy; but he makes no statement about the intensity of shock used by Mr. Heck. If we assume that Mr. Heck used a shock corresponding roughly to that designated as light in Dr. Rhine's data, then the means for the three generations trained by Mr. Heck are very close to what would be expected. They are 80, 70, and 73 errors, respectively, yielding a mean of 75 errors for all three generations together. Dr. Rhine's mean for light shock on the last generation (see Table 1) was 77 errors. The surprising agreement between Heck's results on the three earlier generations and Rhine's results with light shock on the very last generation; and the agreement between McDougall's results on the later generations and the results obtained by Rhine with medium and heavy shocks on the last generation, in connection with McDougall's statement that his own shocks varied

within the limits medium to heavy, raise serious doubt as to whether any of the differences between the means of the ten successive generations reported in the later paper (and these are the only generations for which comparable data are available) can be considered as expressions of genetic differences. Indeed, all these differences could equally well, if not better, be interpreted as due to differences in the intensity of shock administered to the rats.

Although it seems to me highly probable that the increase in facility in successive trained generations was largely due to increase in the strength of shock employed, the same result could have been brought about by inadvertent selection. McDougall found that, without differences in antecedent training, there were still differences in learning ability between different rats; and, further, that differences in learning ability were hereditary. Thus, selection of the more apt would result in increase in facility in the course of generations, without any training at all. McDougall's interpretation of his results, therefore, requires that there should be two separate and distinct ways of producing the same result: increase of facility producible by selection of the more apt and the same result producible by inheritance of the effects of training. Since it is known that selection can be effective and it is highly problematical whether inheritance of the effects of training can be effective, it seems possible that the increase in facility found in the experiment may be due to the method known to be effective.

The method employed to prevent favorable selection was to select at random usually two individuals from each litter before training began; these animals were then trained and bred and all litters born after training were equally represented in the selection made for training and breeding in the next generation. One naturally wonders how the two animals selected from each litter were taken at random. Though not mentioned in his published papers, it has been reported that Professor

McDougall stated that this random selection was made by opening the cage and taking the first two animals that came to hand. It has been suggested by an experienced breeder of rats that this procedure made a selection of the most active and clever rats inevitable, because it is always the more active and clever ones that come to the door at once to see what is going on.

There is, moreover, further evidence of selection. In the first place, throughout the experiment, all runts and obviously weakly animals were rejected. Secondly, in the early generations, at least, the presumption is strong that selection was not guarded against as carefully as it was later, because McDougall obtained a new sample of rats for the purpose, as he himself says, of seeing what results would be obtained when *special attention* was given to the matter of selection. This new sample constituted his "control" group. Thus the superiority of the later trained generations to the new "control" stock might well be interpreted as due partly or largely to favorable selection for several generations in the one stock and the careful avoidance of favorable selection from the start in the other stock.

Even in the later trained generations (14th to 23rd) there are several facts which indicate that selection was not completely avoided. In the first place, in each of these generations, as many as three rats were incapacitated by shock from further training and reproduction. Were the rats thus eliminated the worse rats, so far as facility goes? It seems that such must have been the case on the basis of mere chance alone. For, if any particular shock was as likely as any other to result in the incapacitation of a rat, those rats that required most shocks in order to learn would be more likely to get one of these specially severe shocks than those which learned quickly. Obviously, rats which learned after three shocks would have much less chance of receiving such an unfortunate shock than those which required three hundred shocks. It seems probable that the rats eliminated

in each generation by fatal shocks were, on the average, the worse rats.

Furthermore, there is clear evidence that not all the individuals trained in any one generation were represented by descendants in the next generation. From the data presented by McDougall, there is no way of telling whether the ones thus eliminated were the worse ones, the better ones, or intermediate ones. McDougall merely states that "all litters born of trained parents were equally represented in the next generation." The question then arises: did all trained parents produce litters? This question can be definitely answered for the 11th, 13th, and 21st generations. In order for every individual to be represented by at least one descendant, the number of individuals trained in the parent generation must have been not more than twice the number trained in the next generation. For, if the sexes are equally represented among the parents, then the least number of matings possible which includes all parents is half the number of the parents; so that the least number of litters is also half the number of the parents, and if only one individual is selected from each litter, the least number of offspring is also half the number of the parents. If the sexes were not equally represented in the parent generation, there would have to be a correspondingly greater number of matings, litters and offspring for each parent to be represented by at least one descendant. McDougall does not state the distribution of the sexes in his groups, but granting the best possible case, namely an equal representation of the sexes and the representation of each parent by only one descendant, it is still possible to demonstrate that some trained parents must have been unrepresented by descendants. Thus, there were 41 animals trained in the 11th generation and only 16 in the 12th generation. So that, at the very best, not more than 32 of the 41 animals trained in the 11th generation were represented by progeny. Similarly, from the facts that 23 animals were trained in the 13th generation and 10 in the 14th generation, it can be stated with certainty that

at least three of the 23 animals trained in the 13th generation were not represented by progeny. Likewise, it can be shown that at least 2 of the 34 rats trained in the 21st generation were not represented by progeny.

The preceding calculations are based on the assumption that only one individual from each litter was trained. McDougall states that usually two individuals from each litter were trained. If two individuals were trained, then the number of trained rats in any generation should at least equal the number trained in the preceding generation in order to give equal representation to all trained parents. On this basis, at least 25 of the 41 animals of the 11th generation, 13 of the 23 animals of the 13th generation, 4 of the 10 animals of the 15th generation, 6 of the 22 animals of the 18th generation, and 18 of the 34 animals of the 21st generation were not represented by progeny.

Thus, it is definitely certain that some trained individuals of some generations were not represented by trained descendants and it is highly probable that many more were not. The question of importance is: Which ones were not represented? McDougall states that either the individuals to be bred were chosen before training began or the best and worst rats of each litter were selected to be parents of the next generation. Nevertheless, it is highly desirable to know what the records of the previously chosen rats actually turned out to be. In the major experiment, pedigrees are not given so that it remains uncertain as to how great a part inadvertent selection played.

Some light on the importance of selection may be expected in McDougall's next report, because he is now conducting what promises to be an illuminating experiment. He is deliberately selecting the worse half of the animals in each generation to be the parents of the next generation. As he quite justly feels, a marked increase in facility in successive generations even against strongly unfavorable selection will be strong evidence for his claims of Lamarckian transmission.

As the work now stands, however, there is one point (already briefly mentioned above) that requires further consideration, namely the very great difference between the later trained generations and the "controls." It has already been pointed out that selection among early generations of trained rats and careful avoidance of selection among "controls" might account for much of this difference (see page 547). McDougall ascribes this, however, to the effect of many generations of training, on the one hand, as opposed to few generations of training, on the other hand. This conclusion is based on the assumption that the "control" and experimental stocks were genetically similar with respect to the characteristics upon which facility in their task depends. In support of this assumption there is only the fact that the control stock was obtained, as was the experimental stock, from the Wistar Institute Standard Inbred Stock. The former, however, were obtained in 1927, the latter, in 1920. For seven years the two stocks were bred hundreds of miles apart.

It is, of course, not at all clear that the two stocks were genetically identical with respect to the characteristics in question, even in 1920. McDougall found large differences between individuals and between families in these respects in the early generations of his experimental stock. There are, moreover, no data for the early generations of the experimental stock that are strictly comparable with those obtained seven years later in the "control" stock. The conclusions drawn from a comparison of these two stocks are thus subject to serious criticism.

In the continuation of his work it is to be hoped that Professor McDougall will be able to give a definite experimental answer to each of the alternative interpretations that have been suggested by his critics. Happily, each of these criticisms is susceptible of definite experimental test. Only when these have been made can his very important conclusions be considered as fully borne out by his evidence.

## SHORTER ARTICLES AND DISCUSSION

### PARASYNAPSIS AND APPARENT CHIASMA FORMATION IN *OENOTHERA*

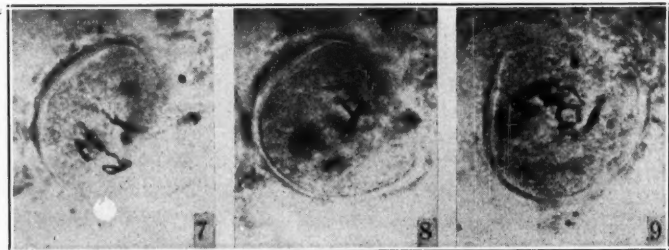
THE behavior of the chromosomes of *Oenothera* during the second contraction in the prophase of meiosis is rather obscure. Various authors (Cleland, 1922, 1924, etc.; Håkansson, 1928; Weier, 1930; Leliveld, 1931; and others) agree that the chromatic threads thicken greatly during this contraction from which the fully formed "diakinesis" chromosomes eventually emerge. During this process the identity of the chromosomes as individuals is obscured by the massing of threads. It is believed by some authors (Håkansson, 1926; Cleland, 1926; Illick, 1929) that the two sides of the loops thrown out from the second contraction knot may represent side-by-side pairing of homologous (parts of) chromosomes, but it is impossible from the figures seen to determine the extent of individual chromosomes. My own observations on various species of *Oenothera* agree with those of the other investigators except for the case to be described.

In a permanent smear preparation (Nawaschin, crystal violet) of a single bud of an *Oenothera* species not yet described, the microspore mother cells were in various stages ranging from early second contraction through late "diakinesis." The diakinesis figures showed that this plant had seven free pairs of chromosomes. In six cells from a single pollen sac the chromosomes, which were in a comparatively thin thread-like stage, were more or less evenly distributed throughout the nucleus so that they appeared distinct and separate. These chromosomes showed a marked side-by-side pairing. They strongly resembled typical parasynaptic chromosomes of a corresponding stage in other organisms. Chromosomes of these six nuclei are illustrated in Figs. 1 to 6 and in the photomicrographs.

There was some evidence (see especially Fig. 1-a) that the chromosomes were in the four-strand stage. Such appearances are difficult to illustrate accurately, and I am not convinced that the figures conclusively showed this condition. Appearances of chiasmata were evident, but it seems impossible in this material to be sure that they actually are true chiasmata (*i.e.*, a cross



FIGS. 1 to 6. Camera lucida drawings ( $\times 2600$ ) of chromosomes of six nuclei showing parasynaptic conjugation.



FIGS. 7 and 8. Photomicrographs of the nucleus drawn in Fig. 2.  
 FIG. 9. Photomicrograph of some of the chromosomes drawn in Fig. 1  
 (all  $\times 880$ ).

between two of four strands). In another cell of the same pollen sac appearances of chiasmata were noted, but in this case the chromosomes were much thinner and longer and it was impossible to determine the extent of any chromosome pair.

The six nuclei referred to were in a stage generally included in late second contraction. The features described for these cells are not ordinarily discernible because of the massing of the threads about the nucleolus. It is probable that these features occur commonly in all *Oenotheras* and were seen distinctly in this case only because the preparation was unusually favorable.

In the published literature of the *Oenotheras* there is a single figure that shows the features described here (Håkansson, 1928, Fig. 2-d). This figure represents a megaspore mother cell of *Oe. Lamarckiana*, which had a ring of 12 chromosomes and one free pair. The free pair shows strong side-by-side pairing with appearances of chiasmata. Certain arms of the ring chromosomes which project from the knot illustrate a similar condition which by analogy may be taken to represent parasynaptic pairing of the homologous regions of the chromosomes constituting the ring. This interpretation was tentatively advanced by Håkansson.

Håkansson (*loc. cit.*) found seven to be the maximum number of loops thrown out from the second contraction knot in the megaspore mother cells of *Oe. Lamarckiana*, while Weier (1930) found thirteen such loops in the pollen mother cells of the same species. Both authors conclude that the constriction between two adjacent chromosomes of the ring should occur approximately in the middle of the loop. It seems to me that one should not expect to find a constant number of such loops in these figures, since some of the loops should be included in the relatively large amount of chromatin in the tighter part of the knot. If one could obtain figures of *Lamarckiana* showing all the chromosomes as distinctly as they were seen in figures of another species reported in this paper, he might expect to find a star-shaped structure with twelve arms and a free pair (see discussion of Belling's translocation hypothesis in Darlington, 1929, and in Emerson, 1931a). Genetical findings have shown that crossing over occurs both in pairing chromosomes and in chromosomes in large rings (Shull, 1923a, b; Emerson, 1931a, b). It follows, on the assumption that chiasma formation and crossing over are related phenomena, that appearances of chiasmata

should be found in arms of the ring chromosomes (during second contraction) as well as in the pairing chromosomes. The figure of *Oe. Lamarckiana* found by Håkansson (referred to above) is in agreement with this expectation.

In connection with such rarely observed parasynapsis in *Oenothera*, it should be remembered that Schwemmle (1926) found indications of parasynapsis in one series of preparations in *Eucharidium* in which the various processes connected with reduction progressed slowly, while in another series, in which the process was more rapid, only the "telosynaptic" appearances commonly found in *Oenothera* were observed.

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### CHROMOSOME STRUCTURE IN *DROSOPHILA*<sup>1</sup>

THE findings of Muller and Painter (1), Painter and Muller (2), and Dobzhansky (3, 4, 5) to the effect that discrepancies occur between the genetical and cytological maps of *Drosophila melanogaster*, recommends a critical study of the organization of the chromosomes of that genus. The present writer has applied, therefore, to *Drosophila* those methods found satisfactory for the preservation of the more intimate details of the structure of plant chromosomes (6). Two species of *Drosophila* have been studied, *D. melanogaster* and *D. virilis*. Chromosomes of somatic and meiotic mitoses have been investigated, but especial attention has been directed to the organization of the spiremes in such large nuclei as those of the salivary glands. The present report will be followed by a more detailed account.

Well-fixed somatic nuclei show the spiremes to be composed of two optically differentiated substances, designated as chromatic and achromatic. The latter stains faintly with iron hematoxylin; the former is, by contrast, hematoxylin avid. Many preparations reveal the spireme as apparently discoid, with alternating bands of chromatic and achromatic material. A similar observation has recently been made by Kostoff (7) in *D. melanogaster*. Although the chromatic cross-striations often appear as single bands, favorable technique reveals that this aspect is due to the close approximation or lateral fusion of a pair of narrow threads. Both single and double bands are portrayed in Figs. 1A and 1D, the former a portion of the spireme of *D. virilis*, the latter of *D. melanogaster*. In other preparations, or even in other por-

<sup>1</sup> Presented to the Biological Section of the Alabama Academy of Sciences, March 13, 1931.

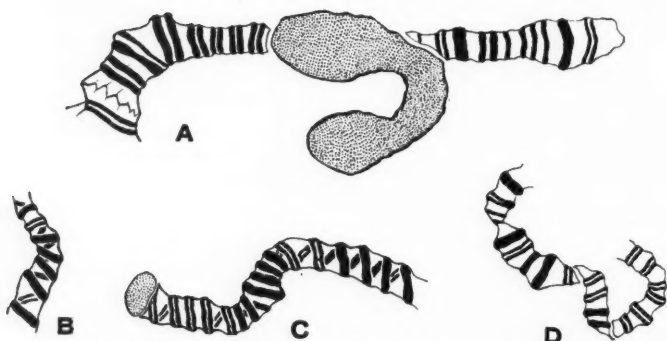


FIG. 1. Structure of the spireme in *Drosophila*. A—indications of cross-striations in *D. virilis*; B—chromonemata in *D. melanogaster*; C—chromonemata in *D. virilis*; D—cross-striations in *D. melanogaster*. B and C are regarded as presenting a more accurate picture of the normal structure than A and D. All from camera-lucida drawings.

tions of some nuclei in which the discoid appearance is observed, the continuity of the chromatic material is evident, in the form of parallel spiral bands. These are embedded peripherally in the achromatic matrix. Figs. 1B and 1C illustrate such organization in portions of the spiremes of *D. melanogaster* and *D. virilis*, respectively. It will be noted in both of the figures that the double spirals are fused in places, to give the appearance of a single thread. Because of the continuity which they maintain, the chromonemata are assumed to represent the gene-carrying material, a possibility suggested by Muller in 1916 (8).

The probable relationship of cross-striations to chromonemata has been discussed extensively by several writers, particularly in reference to the spireme in the salivary glands of the dipteran, *Chironomus*, and to the arrangement of the chromatic material in the monocotyledon, *Tradescantia*. Without renewing the arguments presented elsewhere (9), it is the opinion of the writer, based on a critical study of the chromonemata in plant chromosomes, as well as in *Drosophila*, that the appearance of the discoid or discontinuous structure is the expression of an inadequate technique, the spiral bands presenting a more accurate picture of the normal arrangement of the chromatic material.

It has not been possible to trace the chromonemata through the entire mitosis, as the writer has done in several plants, because the more compact metaphase and anaphase chromosomes of

*Drosophila* do not reveal distinctly their internal structure. However, the moniliform outline, and a median vacuolar region occasionally seen in these chromosomes, suggest the presence of spiral bands. Such intimations of internal organization are commonly viewed in metaphase and anaphase plant chromosomes, although more favorable preparations disclose the chromonemata at these stages.

The presence of chromonemata in *Drosophila* may aid in explaining the discrepancies between the genetical and the cytological maps. If, at the time of crossing-over, when the genetical maps are determined, the chromonemata are entirely extended, or nearly so, and if in the more compact chromosomes, from which the cytological maps are determined, the chromonemata are tightly or unevenly coiled, there is presented a mechanism which permits the maintenance of the linear order of the genes and at the same time allows considerable variation in the scale of their distribution from one region of the chromosome to another. Translocations, as seen in metaphase plates, could therefore be of slight size visibly and yet contain a relatively large portion of a very tightly coiled thread. Conversely, a larger fragment with a loosely wound or extended thread, might represent only a few units genetically. Certainly the coils, where discernible, vary considerably in pitch from one region to another. This factor, coupled with those variations in the diameter of the chromosome, and consequently in the helix during different turns (see Fig. 1), suggests the possibility of considerable variation between measurements made along the chromonemata and those made along the greater axis of the chromosome.

Dobzhansky (4), commenting on the fact that the third chromosome of *D. melanogaster*, when seen cytologically, appears thinner at the middle and rather thickened at the ends, states, "This may suggest that the distances between the genes located far from the spindle fiber are shorter when the chromosome is in the metaphase-plate stage than they are in the stage when crossing-over takes place." Whether the discrepancy between genetical and cytological maps is too great to be accounted for by the different diameters of the different parts of the third chromosome, as Dobzhansky (3) concludes, remains to be investigated in the distribution of the chromonemata in that chromosome.

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THE MULTIPLE SOMATIC EFFECTS OF THE BAR  
GENE IN *DROSOPHILA MELANOGASTER*<sup>1</sup>

## INTRODUCTION

As a result of the extensive studies on the character "bar" eye of *Drosophila*, carried on in this laboratory, and the tendency which was noted for this stock to revert to full or mutate to ultra-bar, the question arose as to the exact extent of the somatic changes produced by a change in this gene. When the germline that produces the bar eye is lost, or doubled, what other parts of the body are correlated with this change? What are the multiple effects of the single gene?

Grateful acknowledgment is here made to Dr. Charles Zeleny, of the University of Illinois, for his suggestions and for the opportunity to work on this problem under his guidance; to Dr. David H. Thompson, of the Natural History Survey, for helpful criticisms and permission to use unpublished data; to Dr. A. H. Sturtevant, of the California Institute of Technology, for the bar stocks used in the experiment (since the writer was in California during part of the course of selection of the stocks); and to Dr. Theodor Dobzhansky for the forked bar and the forked ultra-bar which he had derived from it for his own experiments.

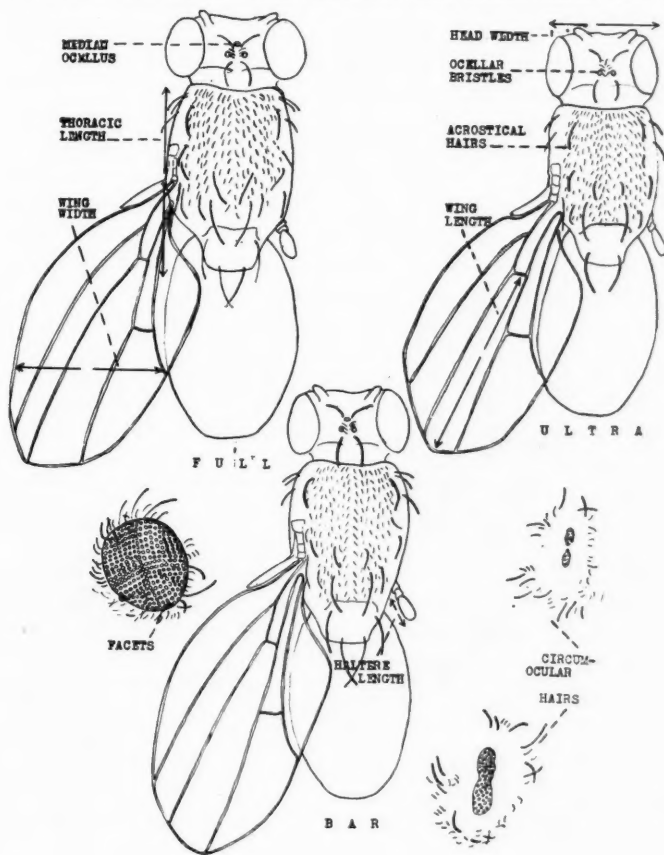
## MATERIALS AND METHODS

The material used in this investigation consisted of two strains of red-eyed bar flies—one with straight bristles and one in which the bristles were forked. From each strain, mutations to ultra-bar and reversions to the full or normal-eyed condition were

<sup>1</sup> Contribution from the Zoological Laboratory of the University of Illinois, No. 397.

obtained, and stocks established so that it was possible to check the results obtained with one series against the other.

The problem under discussion is concerned only with the somatic effects and no effort was made to demonstrate any physiological relationship between the bar genes and the condition of ultra-bar (which Sturtevant calls "double-bar") or reverted full, which is attributed to the absence of the bar gene. The somatic determinations were checked against facet count, and consisted of measurements of different parts of the body—such as head width, wing length and width, haltere length; bristle counts of rows of acrostical hairs, circumocular and ocellar hairs; also a



determination of the proportionate size of the median ocellus, which fluctuates as compared with the two lateral ocelli which do not change.

While it is obviously impossible to eliminate *all* the modifying factors, or to prevent new modifiers from arising during the course of an experiment, the stocks were rendered as homogeneous as possible by inbreeding for the bar strains, and by taking the most recent mutations or reversions for the ultra and full-eyed groups.

Parent flies were bred at 25° C. and the experimental offspring from such parents were isolated, as they emerged, and made up in pair matings for each eight-dram vial for the full and bar-eyed strains; with two-pair matings for the ultra-bar because of its lower fertility. An effort was made to have all the flies used of the same age, thereby minimizing the factor of age. The flies were placed in the 27° incubator after they had been transferred to fresh food, the media used being banana-agar with a pinch of dry Yeast Foam; and as soon as the number of eggs laid in any one vial approached twenty, the parents were removed. More than twenty flies in this size vial results in overcrowding and unsatisfactory food conditions for the larva (as shown by Eigenbrodt and others); while fewer than that number are unable to keep down the growth of the yeast long enough for their own developmental period.

As soon as the larvae had pupated and new flies hatched out, they were isolated and preserved in 75 per cent. alcohol. All counts and measurements were made on flies which had been so preserved.

In all, 100 flies were counted from each stock, 50 males and 50 females, and the averages given are the results of these measurements.

The possible source of error due to the development of accessory modifiers during the course of the experiment has been mentioned. The temperature was controlled automatically and was subject to a change of less than 0.5° C. in either direction from 27°. In order to reduce the personal error, recounts and checks were made on a great many of the measurements.

#### RESULTS

The results of this study are summarized in the accompanying tables, which have been arranged so that a comparison is made

between the females of the straight and forked strains, and in like manner the males—instead of comparing the males with the females in each group, as there is a marked sexual dimorphism.

Since the original difference observed between the several strains was the number of facets each possessed, facet count has been taken as the basis for comparison. Full, bar and ultra flies are sharply marked off from each other, with no overlapping in facet number. The facet count of the females is noticeably less than that of the males. The forked strain closely approaches the straight-bristled stock in this respect.

Correlated with facet count is the width of the head, since the entire head width is measured and this is increased by the size of the compound eyes in full. The full-eyed flies of both sexes had a much greater head width than the bar or ultra-bar flies.

TABLE I  
AVERAGES BASED ON MEASUREMENTS OF 100 FLIES—50 MALES AND 50  
FEMALES FROM EACH STOCK  
(In units of 18.4 microns)

	Facet counts	Head width	Haltere length	Thoracic length	Wing width
♀ ♀					
Full .....	700	47.88 ± .17	14.12 ± .06	56.56 ± .15	51.70 ± .14
Bar .....	65.18 ± .71	37.92 ± .15	13.84 ± .10	53.52 ± .28	51.16 ± .21
Ultra .....	16.84 ± .35	34.66 ± .10	13.46 ± .08	49.38 ± .32	48.82 ± .21
Forked Full .....	700	45.92 ± .14	14.14 ± .07	54.94 ± .24	51.30 ± .11
“ Bar .....	62.98 ± .66	35.54 ± .11	13.56 ± .10	53.22 ± .16	49.94 ± .16
“ Ultra .....	17.30 ± .38	34.62 ± .16	13.00 ± .07	49.88 ± .22	47.60 ± .24
♂ ♂					
Full .....	750	43.72 ± 1.60	13.82 ± .07	49.14 ± .01	45.80 ± .13
Bar .....	99.30 ± .81	35.16 ± .13	13.56 ± .06	46.94 ± .22	44.88 ± .18
Ultra .....	18.78 ± .20	32.20 ± .09	12.54 ± .13	44.46 ± .22	43.80 ± .15
Forked Full .....	750	42.64 ± 1.47	13.74 ± .09	48.92 ± .26	45.74 ± .13
“ Bar .....	87.44 ± .09	34.02 ± .11	13.14 ± .05	46.60 ± .20	44.70 ± .16
“ Ultra .....	19.78 ± .38	32.18 ± .11	12.66 ± .09	45.50 ± .16	43.72 ± .16

The haltere length of bar again places it in an intermediate position between full and ultra, although the forked and straight-bristled strains are nearer together here than in any other single measurement.

Sexual dimorphism is shown by a comparison of the size of the males and females of all groups. Particularly does thoracic length contribute to making the females much larger than the males. Correlated with the thoracic length is the size of the wings—especially the wing length.

Wing width was measured to include its greatest diameter from the Vth longitudinal vein to a point directly across and at right angles to its length. The wing length was measured from the anterior cross-vein to the tip of the IIIrd longitudinal.

TABLE II  
AVERAGES BASED ON MEASUREMENTS OF 100 FLIES—50 MALES AND 50  
FEMALES FROM EACH STOCK

	Wing length	Ocellar hair number	Circum- ocular hairs	Acrostical hair number	Size of median ocellus
♀ ♀					
Full .....	76.24	6.26	53.90	16.54	.93
	± .22	± .04	± .14	± .10	
Bar .....	73.62	6.88	49.86	17.60	.73
	± .30	± .09	± .29	± .11	
Ultra .....	72.62	7.14	45.40	18.06	.05
	± .32	± .11	± .31	± .07	
Forked Full .....	76.20	5.84	43.10	15.94	.91
	± .18	± .08	± .13	± .07	
“ Bar .....	73.40	6.30	39.16	16.24	.74
	± .32	± .06	± .15	± .13	
“ Ultra .....	72.56	6.68	36.66	16.58	.12
	± .30	± .13	± .28	± .58	
♂ ♂					
Full .....	67.12	5.96	52.14	16.28	.82
	± .20	± .68	± .11	± .05	
Bar .....	65.28	6.30	47.78	17.72	.68
	± .30	± .05	± .26	± .10	
Ultra .....	64.20	6.88	43.12	18.02	.05
	± .29	± .11	± .28	± .07	
Forked Full .....	67.12	5.88	40.96	15.96	.93
	± .14	± .08	± .13	± .07	
“ Bar .....	65.20	6.20	38.28	16.22	.84
	± .25	± .06	± .18	± .05	
“ Ultra .....	64.48	6.92	34.96	16.34	.08
	± .17	± .11	± .24	± .04	

The place of the missing ocellus in ultra-bar is not infrequently taken by one or more ocellar hairs; and the number of the latter stands in inverse relationship to the number of facets present.

Essentially the same thing is shown, though to a less striking degree, by the number of rows of aerostical hairs found in the different stocks; while the reverse holds true for the rows of circumocular hairs immediately surrounding the compound eye.

The size of the median ocellus is very closely associated with the factor for bar, so that one can almost tell by *its* size alone to what strain the fly possessing it belongs, since it is largest in full and smallest or even altogether lacking in ultra. The lateral ocelli do not change in size and were used as the basis for comparison, the median ocellus being understood to be in a percentage ratio to the lateral ocellus next to it.

#### CONCLUSIONS

The basis for an interesting speculation as to the extent of the developmental effects of single genes is provided—when the single gene for “bar” produces so marked a change as the reduction in facet count from 700 or more in full to less than a hundred in bar.

The single striking change is in the inhibition of the facet-forming substance, but correlated with it are other less marked, but perfectly definite and consistent somatic changes. As might be expected, these are most pronounced in the head region and in association with the eye itself; the width of the head, which is directly affected by the size of the eye, the size of the median ocellus and the number of ocellar hairs.

One of the criticisms made of the mutation theory of evolution is that it is inconceivable that there should be proper physiological correlation of organs if each part has arisen by an independent mutation. This is based upon a misconception of the extent of the somatic effects produced by a single gene change, for, as may be seen from the data herewith presented, even where one part is especially modified, other effects are evident in a great many parts of the body.

In this case the one known difference between the stocks was the factor governing facet-formation, and evidently the factor which places the bar stock in an intermediate position between full and ultra exerts a similar influence on practically all measurable parts of the body. “Full” predominates in everything

except the ocellar bristle number and the number of rows of aestroscotal hairs. In these latter instances the relationship is reversed, although bar still retains its intermediate place.

Incidentally, in working with the forked and straight-bristled strains certain differences were noted between them.

The conclusions to be drawn from these observations may be summed up as follows: (1) The somatic effect of the bar gene is primarily a reduction in facet number; (2) when this effect is doubled, as in ultra-bar, the facet number is again appreciably reduced; (3) head width, haltere length, thoracic length, wing length and width, and size of the median ocellus are directly correlated with the facet count; (4) while the number of rows of aestroscotal hairs and the ocellar hair number are in inverse relationship; (5) in almost every respect the forked bristled flies are smaller than those with the straight bristles; (6) proof of the wide-spread somatic effects produced by a single gene change is shown by the fact that observations made upon either the forked or straight-bristled strain are substantiated by similar observations upon the other.

RUTH ANDERSON

#### EXPERIMENTALLY INDUCED ALTERATIONS OF THE MORPHOLOGY OF CHROMOSOMES

THE recent experiments with X-radiations (Painter and Muller 1929, Dobzhansky 1929) show that striking alterations in the morphology of chromosomes are obtainable in this way. An analogous treatment was also applied in the Cytological Laboratory of the Institute of Plant Industry (Leningrad) to the seedlings of *Secale cereale*, *Crepis capillaris* and to some other plants with similar results. Fragmentations, losses of chromosome parts, and translocations of parts from one chromosome to another were observed some days after treatment. Three figures selected from among numerous observed conformations may serve as illustration.

In a plate of *Secale cereale* (Fig. 1) two out of 14 chromosomes—consisting normally of two well-developed arms—are provided only with oval heads, which probably represent the remaining parts of their respective arms, the major parts of the latter being lost.



FIG. 1. *Secale cereale*. Nuclear plate from a seedling treated with x-rays. Two chromosomes are provided with heads.

In one plate of a treated *Crepis capillaris* (Fig. 2) chromosome A' shows a newly formed secondary constriction, chromosome D is deprived of the greater part of its large arm, and on the contrary chromosome C' is considerably lengthened—evidently at the expense of the translocated part of chromosome D.

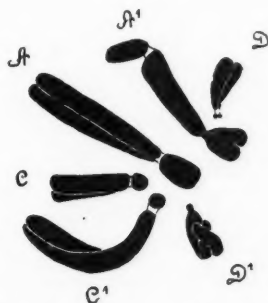


FIG. 2. *Crepis capillaris* Wallr. Nuclear plate of a seedling treated with x-rays. The constrictions are achromatic.

In a second plate of the same species (Fig. 3) the long arm of chromosome A is fragmented. Chromosome A' is fragmented at its constriction. Both separated arms have formed little heads and constrictions and so have turned into two new types of normally constituted chromosomes.



FIG. 3. *Crepis capillaris* Wallr. Nuclear plate of a seedling treated with x-rays.

There is no doubt that various other agents can produce similar effects—as we have found by means of alcohol treatment. The most interesting alteration we have obtained is represented in Fig. 4. Chromosome D' has augmented its head but lost its satellite, chromosome C' on the contrary has diminished its head but acquired a satellite.

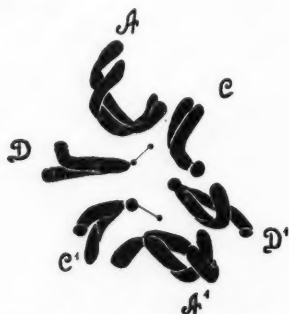


FIG. 4. *Crepis capillaris* Wallr. Nuclear plate of a seedling treated with dilute alcohol.

The chromosome changes described above happen under apparently normal conditions as well. A number of diverse conformations have been observed by us in an individual of *Crepis tectorum*. A rather complex case is represented in Fig. 5. One sees here 10 chromosomes instead of 8—some of them being short fragments, which are nevertheless provided with constrictions and heads.



Fig. 5. *Crepis tectorum* L. Altered nuclear plate from a plant grown under apparently normal conditions.

It therefore seems quite reasonable to suppose that large and sudden alterations of chromosome morphology can take place in the process of evolution.

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#### THE EFFICIENCY OF THE CORRELATION COEFFICIENT FOR ESTIMATING LINKAGE INTENSITIES

A SEARCH for a rapid and reliable method for estimating linkage intensities led Y. Takezaki (6) in 1925 to propose a formula based on the method of treating the fourfold table of phenotypic frequencies as a correlation table. Working quite independently, F. V. Owen (5) developed the same method in 1928. Both authors presented tables to facilitate the rapid calculation of linkages by this method.

In the  $F_2$  generation of a cross between parents with two factor pairs differing there are to be expected, normally, four classes of zygotes. These may be designated AB, Ab, aB and ab. If the number of individuals obtained in each of these four classes is designated as a, b, c and d, respectively, and the total number observed as n, the value of  $r^2$  (derived originally for

the fourfold table by Boas (1), Johannsen (4) and Yule (7) is given by

$$r^2 = \frac{(ad - bc)^2}{(a+b)(c+d)(a+c)(b+d)} \quad \text{I}$$

For a, b, c and d we may now substitute the values of their expectations in terms of the proportion, p, of the AB and ab gametes, namely

$$\frac{n}{4}(2+p^2, 1-p^2, 1-p^2, p^2)$$

We then have

$$r^2 = \frac{(4p^2 - 1)^2}{9} \quad \text{II}$$

From whence

$$p = \frac{1}{2} \sqrt{3r+1} \quad \text{III}$$

if r is taken to be positive when ad exceeds bc. This is the formula derived by Takezaki (6) and Owen (5).

The cross-over percentage, expressed as a decimal fraction, will then be given directly by p when crosses are made in the repulsion phase and by 1-p when made in the coupling phase.

Takezaki derived a formula for the standard error of his estimate of p from the assumption that the standard error of r, obtained from the fourfold table by equation II, could be equated to the standard error of a correlation coefficient derived from a normal frequency surface having the same number of observations. This mistaken assumption has led to the precision of this method of estimating linkages being greatly overestimated. On Takezaki's assumption the standard error of his estimate of p may be calculated as follows:

The variance of r ( $V_r$ ) from a product moment correlation coefficient is  $\frac{(1-r^2)^2}{n}$

$$V(p^2) = \frac{9}{16} V(r)$$

Then

$$V(p^2) = \frac{9(1-r^2)^2}{16n}$$

To obtain the variance of p we divide the variance of  $p^2$  by  $4p^2$

$$\text{or} \quad V(p) = \frac{9(1-r^2)^2}{64p^2n}$$

And the standard error of p is

$$\frac{3(1-r^2)}{8p\sqrt{n}} \quad \text{IV}$$

Fisher (3, p. 249) has given a general method for calculating the sampling variance (standard deviation squared) and thence the standard error of any estimate expressible explicitly in terms of the frequencies. The method involves the differential coefficients of the function in question with respect to each observed frequency and to the total,  $n$ . Applying this method to the problem of deriving the true standard error of  $p$  we proceed as follows:

$$V(r) = V \left\{ \frac{ad - bc}{\sqrt{(a+b)(a+c)(b+d)(c+d)}} \right\}$$

Substituting in the general equation (3)

$$\frac{1}{n} V(r) = S \left\{ p \left( \frac{\partial r}{\partial a} \right)^2 \right\} - \left( \frac{\partial r}{\partial n} \right)^2 \quad V$$

where  $r$  is the value calculated from the fourfold table and  $p$  is here, for each class of zygotes, the probability of an  $F_2$  individual falling in that class. Differentiating, we obtain

$$\begin{aligned} \frac{\partial r}{\partial a} &= \frac{d}{\sqrt{(a+b)(a+c)(b+d)(c+d)}} - \left\{ \frac{ad - bc}{(a+b)(a+c)(b+d)(c+d)} \right. \\ &\quad \left. - \frac{(a+b+a+c)(b+d)(c+d)}{2\sqrt{(a+b)(a+c)(b+d)(c+d)}} \right\} \\ &= \frac{d}{\sqrt{(a+b)(a+c)(b+d)(c+d)}} - \frac{1}{2} r \left( \frac{1}{a+b} + \frac{1}{a+c} \right) \quad \text{VI} \end{aligned}$$

$$\frac{\partial r}{\partial b} = \frac{-c}{\sqrt{(a+b)(a+c)(b+d)(c+d)}} - \frac{1}{2} r \left( \frac{1}{a+b} + \frac{1}{b+d} \right) \quad \text{VII}$$

$$\frac{\partial r}{\partial c} = \frac{-b}{\sqrt{(a+b)(a+c)(b+d)(c+d)}} - \frac{1}{2} r \left( \frac{1}{a+c} + \frac{1}{c+d} \right) \quad \text{VIII}$$

$$\frac{\partial r}{\partial d} = \frac{a}{\sqrt{(a+b)(a+c)(b+d)(c+d)}} - \frac{1}{2} r \left( \frac{1}{b+d} + \frac{1}{c+d} \right) \quad \text{IX}$$

Since the expected frequencies in the four classes are equal to

$$n \left\{ \frac{2+\theta}{4}, \frac{1-\theta}{4}, \frac{1-\theta}{4} \text{ and } \frac{\theta}{4} \right\},$$

where  $\theta = p^2$ , we now substitute these values for  $a, b, c$  and  $d$  in equations VI, VII, VIII and IX, respectively, and obtain

$$\frac{4\theta}{3n} - \frac{2}{n} \left( \frac{4\theta-1}{3} \right) \frac{2}{3} = \frac{4(1-\theta)}{9n} \quad \text{X}$$

$$-\frac{4(1-\theta)}{3n} - \frac{2}{n} \left( \frac{4\theta-1}{3} \right) \frac{4}{3} = -\frac{4(1+5\theta)}{9n} \quad \text{XI}$$

$$-\frac{4(1-\theta)}{3n} - \frac{2}{n} \left( \frac{4\theta-1}{3} \right) \frac{4}{3} = -\frac{4(1+5\theta)}{9n} \quad \text{XII}$$

$$\frac{4(2+\theta)}{3n} - \frac{2}{n} \left( \frac{4\theta-1}{3} \right) 2 = \frac{4(9-9\theta)}{9n} \quad \text{XIII}$$

Since  $n$  does not appear explicitly  $\frac{\partial r}{\partial n} = 0$ . Substituting the values in equations X to XIII in equation V, squaring and multiplying by the expected frequencies

$$\frac{1}{n} V(r) = \left(\frac{4}{9n}\right) \frac{1}{4} \left\{ (1-\theta)^2 (2+\theta) + 2 (1-\theta) (1+5\theta)^2 + 81\theta (1-\theta)^2 \right\}$$

$$\text{or} \quad V(r) = \frac{16}{81n} (1-\theta) (1+25\theta-8\theta^2)$$

$$\text{Since} \quad V(\theta) = \frac{9}{16} V(r)$$

$$V(\theta) = \frac{(1-\theta) (1+25\theta-8\theta^2)}{9n}$$

The variance of  $\sqrt{\hat{\theta}}$  or  $p$ , will then be

$$\frac{V(\theta)}{4\theta} \quad \text{or} \quad \frac{(1-\theta) (1+25\theta-8\theta^2)}{36n\theta} \quad \text{XIV}$$

and the standard error of  $p$  may then be expressed conveniently

$$\text{as} \quad \sqrt{\frac{(1-p^2) (1+25p^2-8p^4)}{36np^2}} \quad \text{XV}$$

Fisher (2) has also shown that the method of maximum likelihood, in the theory of large samples, will in all cases give a standard error as small as possible. The efficiency of the correlation method can then be tested by dividing the variance for the maximum likelihood method (3, p. 250) by that of the correlation method. This quantity,

$$\frac{2\theta (1-\theta) (2+\theta)}{(1+2\theta)n} \div \frac{(1-\theta) (1+25\theta-8\theta^2)}{9n} = \frac{18\theta (2+\theta)}{(1+2\theta) (1+25\theta-8\theta^2)} \quad \text{XVI}$$

will then give a measure of the efficiency of the correlation method for all values of  $\hat{\theta}$  ( $=p^2$ ). The result is shown graphically in Fig. 1, as well as the apparent efficiency given by the sampling error deduced on the assumption of a normal correlation surface as given in equation IV.

It is seen readily that the curve for the actual efficiency of the correlation method calculated from the correct formula, equation XV, does not exceed 100 per cent. for any possible values of  $p$ , from 0 to 1, in accordance with the general theory. The correlation method is fairly efficient in the coupling phase and for loose linkage in repulsion. For close linkage in repulsion it is not efficient. Since there are other formulae (3), such as the maximum likelihood method and the product ratio method, which are efficient for all values of  $p$ , it would seem preferable to use these formulae in most cases.

The error formula based on the incorrect method of treating the fourfold table of phenotypic frequencies as a normal frequency surface gives more than 100 per cent. efficiency in the coupling phase, which is obviously impossible. It is only for the value of  $p = .50$  that this formula is correct.

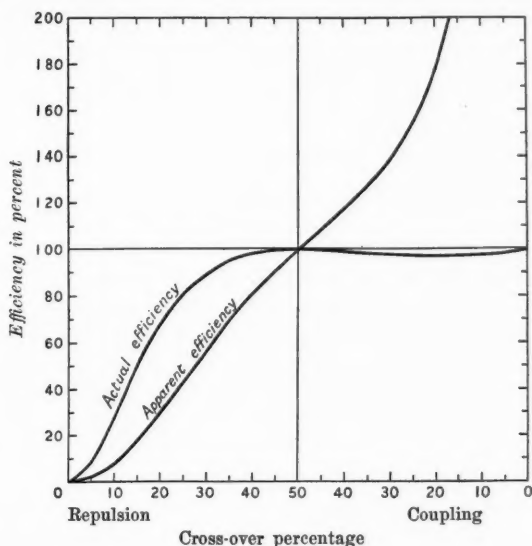


FIG. 1

Graph showing actual efficiency of correlation method for estimating linkage intensities and its apparent efficiency when the standard error of the correlation is incorrectly calculated.

For close linkage in coupling the two recombination classes,  $b$  and  $c$ , may be very small. In fact, recombinations in  $b$  or  $c$  may be entirely lacking. Under such conditions the theory of large samples breaks down and some of the efficient statistics fail. For close linkage  $b$  and  $c$  will be small numbers, either of which may be zero, while  $a$  and  $d$  will be approximately  $\frac{3}{4}$  and  $\frac{1}{4}$  of the sample respectively.

If  $b$  and  $c$  are small compared with  $a$  and  $d$ , then  $r$  may be expressed as

$$\left(1 - \frac{bc}{ad}\right) \left(1 - \frac{1}{2} \frac{b}{a} + \dots\right) \left(1 - \frac{1}{2} \frac{c}{a} + \dots\right) \left(1 - \frac{1}{2} \frac{c}{d} + \dots\right) \left(1 - \frac{1}{2} \frac{b}{d} + \dots\right) \\ = 1 - \frac{1}{2} (b+c) \left(\frac{1}{a} + \frac{1}{d}\right),$$

neglecting squares and products of  $\frac{b}{a}$ , etc.

Then

$$p = \frac{1}{2} \sqrt{4 - 3/2 (b+c) \left(\frac{1}{a} + \frac{1}{d}\right)} \\ = 1 - 3/16 (b+c) \left(\frac{1}{a} + \frac{1}{d}\right)$$

to the same approximation. Putting the limiting values  $a = \frac{3}{4}n$  and  $d = \frac{1}{4}n$  in the expression,  $p = 1 - \frac{b+c}{n}$ . This is the same result as is given for this case by Emerson's method and by maximum likelihood.

Contrast the product method

$$\frac{(1-p^2)^2}{p^2(2+p^2)} = \frac{bc}{ad}$$

When  $b$  is 0 and  $c$  is not, cross-overs must have occurred, and yet  $1-p$  is estimated to be exactly zero, which is manifestly wrong. It would seem, therefore, that the product ratio method should not be used when the observed numbers in the  $b$  and  $c$  classes are very small, *i.e.*, less than a total of about ten. For very close linkages in coupling when  $b$  and  $c$  are small the maximum likelihood, Emerson's or the correlation method would be preferable to the product ratio. The maximum likelihood method might claim a theoretical advantage since it is efficient for all values of  $p$ .

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<sup>1</sup> The writer takes great pleasure in expressing his appreciation to Dr. R. A. Fisher for assistance in the derivation of the formulae presented here.

ON THE OCCURRENCE OF *TRICHOCORIXA* KIRKALDY  
(CORIXIDAE, HEMIPTERA-HETEROPTERA)  
IN SALT WATER AND ITS ZOO-GEO-  
GRAPHICAL SIGNIFICANCE

IN spite of the considerable literature on the mechanisms by which animals and plants might be dispersed, too little attention has been given to the physiological feasibility of the methods of distribution invoked to explain wide and discontinuous ranges. The following records appear to indicate a case where dispersal by ocean currents is within the limits of physiological possibility and may be legitimately offered as an explanation of a very wide and remarkable distribution.

*Trichocorixa* Kirkaldy is a genus of water-boatmen of wide distribution in South, Central, and southern North America. Several forms are recorded from the West Indies and the genus would appear to have a distribution typical of many groups of Central or South American origin were it not for a single species which ranges right across the Pacific from California to China. The following notes deal with this form, *T. wallengreni* (Stål), and its close Eastern ally, *T. verticalis* (Fieb.).

During fisheries investigations in Delaware Bay in 1929 Mr. Albert E. Parr, curator of the Bingham Oceanographic Foundation, Yale University, obtained two living ♂ specimens of *Trichocorixa verticalis* (Fieb.) associated with typical marine planktonic organisms in tow-nettings taken at stations 48, north of Brandywine Shoal, salinity 24.90 per mille (June 18, 1929) and 63, salinity 29.34 per mille (June 18, 1929). Although drowned flies and other insects were frequently met with in the surface plankton of this region, no specimens of living and apparently healthy insects other than these two corixids were obtained. *T. verticalis* occurs commonly in ponds near the sea in Cape May County, N. J., and is recorded from Connecticut, Pennsylvania, Georgia and the West Indian Islands of Cuba and St. Thomas (Lundblad, 1929).

Mr. Richard M. Bond, Bishop Museum fellow of Yale University, has forwarded for determination a number of specimens of the closely allied *Trichocorixa wallengreni* (Stål) taken in "strong brine from salt works at Elkhorn Slough," Monterey County, Cal. (10th November, 1930). Both sexes as well as immature individuals occurred in this locality, which otherwise is

inhabited only by the typical halobionts *Dunaniella*, *Artemia* and *Ephedra*. *Trichocorixa wallengreni* was originally described from California, but recently Lundblad (1929b) has shown that *Corixa blackburni* Buch.-White from Hawaii is synonymous and has also recorded the species from Shanghai. This transpacific distribution is probably unique among waterbugs; the Hawaiian records strongly suggest that it is to be explained by dispersal across the Pacific Ocean, rather than by an Alaskan-Siberian land-bridge. *T. wallengreni* or its eggs might possibly be transported in damp salt, but the species has clearly been established for some time in Hawaii (*C. blackburni* was described by Buchanan-White in 1877) and a natural method of dispersal seems more probable. Since it is clear that the species can stand salinities considerably above those of the sea it is not inconceivable that specimens might travel by the Northern Equatorial Current from California to Hawaii, and from Hawaii to China. Insects of this family being less dense than water when surrounded by their air bubble, this method of distribution would involve a minimum of effort.<sup>1</sup>

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<sup>1</sup> Since the above was written, Dr. H. B. Hungerford kindly informs me that he has specimens of *Trichocorixa* from the Galapagos Islands and that he has frequently received specimens of the genus "from saline waters. The exact salinity of the water, however, has never been available."

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